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INFLUENCE OF SOCIAL EXPERIENCE ON DEVELOPMENT OF INDIVIDUALS OF ACHETA DOMESTICUS (L.) THE HOUSE CRICKET, AND OF SOME GRYLLUS SPECIES (ORTHOPTERA: GRYLLIDAE)

by

© DOREEN WATLER

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

ENTOMOLOGY DEPARTMENT

EDMONTON, ALBERTA

SPRING, 1979

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Influence of social experience on development of individuals of Acheta domesticus (L.) the house cricket, and of some Gryllus species (Orthoptera: Gryllidae). in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Entomology.

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Abstract

Nymphs of *Acheta domesticus* (L.) tended to group together in clean environments but were more strongly attracted to substrates contaminated by other nymphs or adults. Nymphs in peer groups ate more food per milligram of body weight than those in isolation and converted it to body tissue more efficiently. They had a faster relative growth rate and matured more rapidly, often having one or two fewer instars during development than isolated nymphs, and completed each instar more rapidly. All nymphs weighed at least 96 mg before developing wing-pads.

Nymphs did not detectably increase temperature or humidity in rearing jars. They grew as fast in pairs as in larger groups. They grew as fast with nymphs of *Gryllus fultoni* (Alexander) as with nymphs of their own species, and nearly as fast with nymphs of *G. veletis* (Alexander and Bigelow). Isolated nymphs in contact with substrates contaminated by nymphs of the same age did not grow significantly faster than isolated nymphs. Growth rate and sensitivity to the presence of peers was not affected by parental age.

Isolation part way through development did not retard maturation, but continuous association with an older cricket did so, most retardation occurring in later instars. Nymphs reared with older nymphs (except males reared with older females) were significantly heavier than nymphs reared with

others of their own age.

Grouping partway through development accelerated maturation of females, but not of males. Females reared in groups began egg-laying earlier than those reared in isolation. Grouped females matured faster than males in the same treatment in all experiments but isolated females did not, and there was generally less difference in maturation rate between the sexes in isolated samples.

Grouped nymphs of G. pennsylvanicus (Burmeister), G. fultoni and G. veletis from Indiana did not grow faster than those in isolation. Female nymphs of G. veletis from Alberta grew faster in dense groups than in smaller groups or isolation, but males did not. Macroptery of G. veletis adults of both stocks was strongly and positively correlated with grouped rearing. Very few individuals of G. pennsylvanicus become macropterous whether reared in groups or in isolation.

It was concluded that nymphs did not grow faster in response to the pheromone (or pheromones) which cause them to aggregate. They required the presence of other nymphs, in early instars at least, to do so, and stimulation was probably tactile. Faster food consumption of grouped nymphs may result from social facilitation, which continued after contact between nymphs ceased.

Nymphs in natural populations would have a better chance of survival to maturity if they hatched early and developed quickly, since growth of smaller nymphs would be inhibited by the presence of adults. Shorter pre-oviposition period of females would give their offspring a competitive advantage in the next generation. Faster growth is an advantage only to species which have no obligatory overwintering stage.

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0.0 GENERAL INTRODUCTION

Members of many insect species have predictable responses to the presence or absence of others of their kind. Grouping or isolation may change behavior, physiological parameters or body proportions and may arise over a long period or immediately. Responses are usually manifested when only two members of the species are together, although they may be intensified at higher densities.

Such phenomena were named "grouping effects" (*effet de groupe*) by Grassé, in 1946. He distinguished grouping effects as being responses of one individual to stimuli produced by another, in contrast to "mass effects" which result from changes in the environment caused by presence of a population of animals. He regarded the stimuli as being sensory, and intended his definition to include interactions among members of social species as well as non-social ones.

Our understanding of insect societies has so much advanced since 1946, however, that Grassé's term is now obsolete in its original definition. It is still useful, however, to consider it when discussing interactions between insects which can complete development in isolation, but which are often found in groups in nature. Grouping effects in this sense have been noticed in members of Orthoptera, Dictyoptera, Homoptera and Lepidoptera.

Insects of these species do not co-operate with each other in any organized way, in food-gathering or storage, raising young or building shelters. Their contact with each other may occur only during resting periods, since each forages for itself.

The term "grouping effect" may suggest that living in a group produces unusual reactions in the subjects studied. However, since members of species in which these effects occur are often found in groups in nature, contact with others of their own kind is normal for these insects. Thus, the characteristics they show when grouped are probably the ones most commonly seen in natural conditions. It may be the isolated individuals which experience unusual conditions, and the difference between grouped and isolated subjects might well be called an "isolation effect". To name it a "grouping effect" or "aggregation effect" emphasizes that the phenomenon is often found in members of gregarious species, whose life-cycle is adapted to such situations.

Analysis of such phenomena throws light on biological strategies which are akin to the development of sociality, but distinct from it. Forms that responses to grouping take, and mechanisms by which they are achieved are still at the cataloguing stage. Since their adaptive significance has often not been considered, their adaptive value for an individual is usually unassessed, much less tested.

Chauvin first reported that nymphs of Acheta domesticus (L.) grow faster in groups than in isolation (1946, 1958) and carried out many experiments on the phenomenon. However, his major conclusion, that faster growth occurred in grouped nymphs only if they were the offspring of females more than one month post adult emergence at 30° C, was not supported by his published data, which clearly showed that nymphs from mothers of any age gained weight faster when grouped.

McFarlane (1962) and Charpentier, Larrson and Olofsson (1972) also reported faster growth in grouped nymphs. Johnston and McFarlane (1973) found females to grow faster in groups only if they were the offspring of mothers four weeks or less post adult emergence at 30± 1°C.

The only work which has related grouping during development to subsequent effects in adults was Gona's (1976) study which reported behavioral differences between adult males of A. domesticus reared in groups and in isolation during development. Young adult males isolated either from hatching or from the last nymphal instar were found to be more likely to copulate during a first two-hour exposure to an adult female than were males from a same sex group or males isolated after moulting to adult. Those isolated from the last instar had a significantly longer latency than did those in other treatments, within the two-hour period.

Other differences have been recorded between adults grouped throughout life and those separated from groups either just before or just after the last moult. Nowosielski and Patton (1965) found that crickets isolated from groups within 24 hours of adult emergence were more likely to die in early adulthood than were adults left in groups. But older crickets had a greater life expectancy when kept in isolation. Female life expectancy was especially shortened by living in a mixed sex group, but the opposite was true for males.

Chauvin (1958) considered faster growth rate to be caused by sensory stimuli received by the cerci and antennae, because amputation of either organ reduced the growth rate of both grouped and isolated nymphs. McFarlane (1966 a,b,c, 1967, 1968) found evidence that chemicals absorbed directly into the body influenced growth rate. Neither hypothesis has been further tested by other workers, and very little has been said about the adaptive value of the effect in the life of the insect.

The objectives of my project were to find out why grouped crickets grew faster than isolated ones, and to develop a hypothesis concerning the adaptive value of faster growth in grouped nymphs of A. domesticus.

1.0 IS ACHETA DOMESTICUS A GREGARIOUS SPECIES?

1.1 Introduction to Section 1.0

Grassé defined "gregarism" as a trend to form aggregations by mutual attraction, visual, tactile or olfactory stimuli being the cues used (Brossut, 1975). The tendency of cockroaches and locusts to form aggregations is well-documented (review by Brossut, 1975) but is less well studied in crickets, although members of most species cultured in laboratories are kept in groups.

Sexton and Hess (1968) found that adults of A. domesticus of both sexes were attracted to wooden blocks previously 'conditioned' by crickets in a communal terrarium, and rested on them in preference to clean blocks. However, they were repelled for about 24 hours by the same 'conditioned' blocks wrapped in paper tissue or filter paper, and preferred clean wrapped blocks. The authors concluded that the blocks had had both a stable, non-volatile attractant deposited on them, and an unstable, volatile repellent. Adults of both sexes could condition blocks with both substances, but the repellent produced by the same sex had more effect on an individual.

Otte and Cade (1976) showed that adult males of A. domesticus could distinguish the odour of adult females from that of other males and that they were attracted towards groups of females or to their conditioned filter paper resting sites. The males, which came from all-male adult colonies, and which had not had access to adult females at any time, increased grooming and became aggressive towards each other in the presence of female odour. Adult females were clearly attracted by the odour of other adults, but it was not demonstrated that they could distinguish the sex of other crickets by odour.

The following experiments were carried out to determine if nymphs of A. domesticus are attracted to each other when choosing a place to rest, and if they would form groups actively. I also tested the influence of substrates previously used by crickets on choice of resting site.

1.2 Materials and Methods

Circular cardboard arenas, 40cm high and 45cm in diameter were used (fig. 1). Each had a disposable floor of Whatman's No. 1 filter paper which was replaced for each trial, to which 10 resting sites, of a type proven to be acceptable (fig. 2), were glued in a circle. Each resting site was a 13x5cm strip of Whatman's No. 1 filter paper rolled into a scroll 2cm in diameter. They were as uniform in shape as possible, and were glued to the floor with one open end upwards. They could be inspected without disturbing

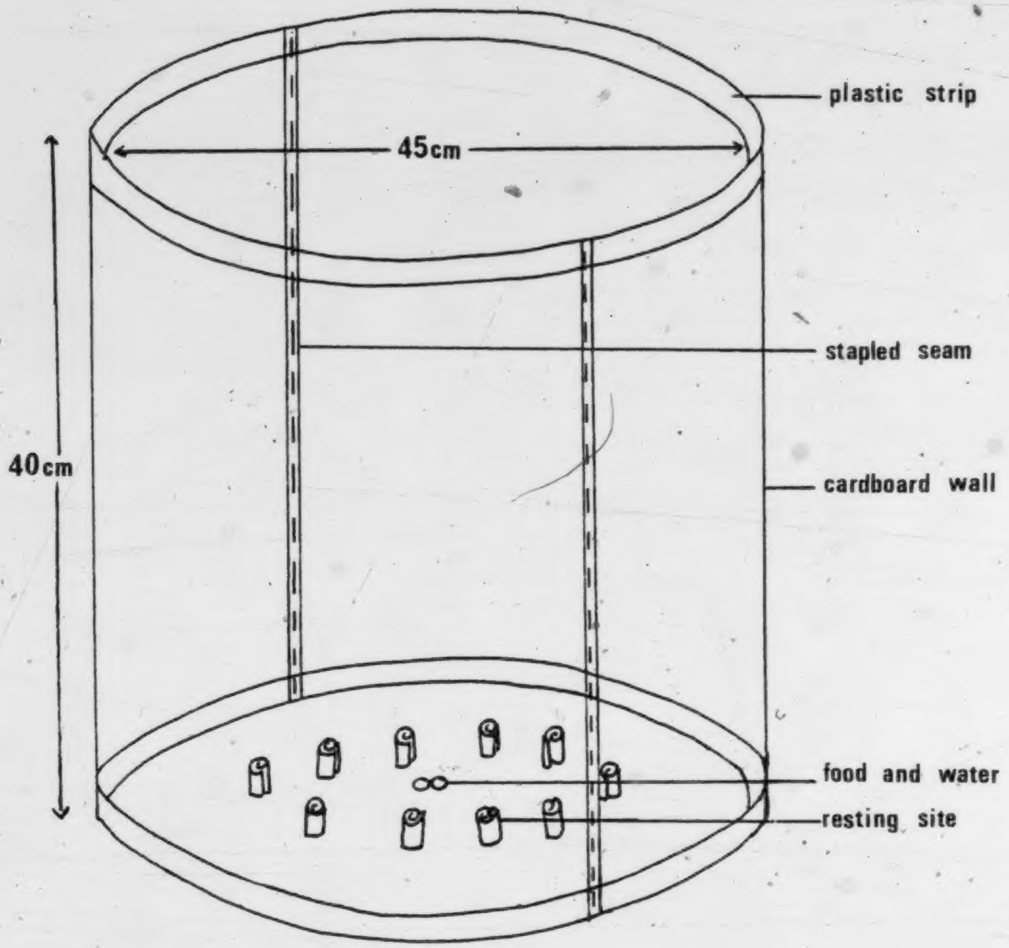
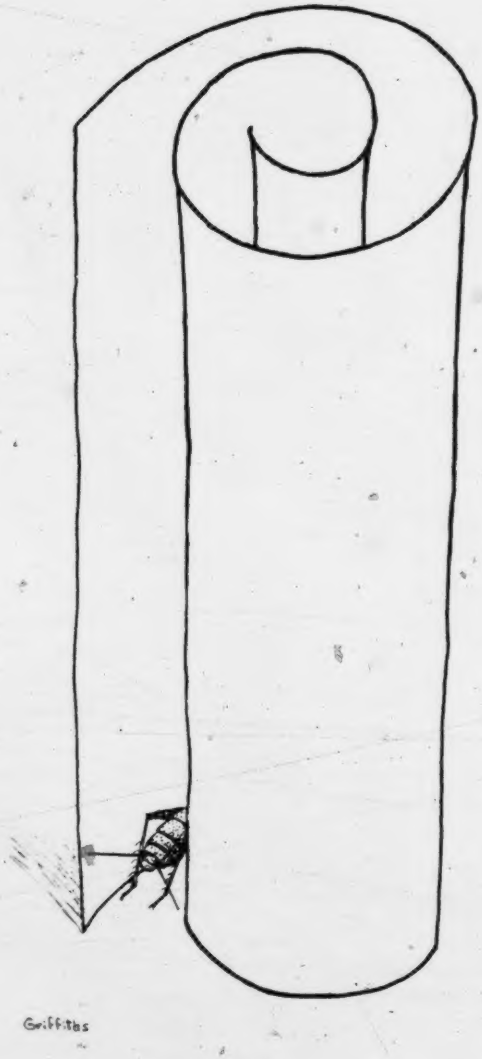

plastic strip
45cm
stapled seam
40cm
cardboard wall
food and water
resting site

Fig. 1. Arena used for aggregation trials.

Fig. 2. Resting site used in aggregation trials.



the crickets, and could not be moved during a test. Food and water were provided in small containers at the centre of the arena. Transparent plastic tape to which crickets could not cling prevented them from climbing the walls of the arena and escaping. Uniform illumination was provided by fluorescent tubes.

Nymphs were selected from a grouped stock, and were tested in pairs at about 25°C. Members of a pair were of the same size and in approximately the same stage of the moult cycle. Nymphs used were in all instars from fourth to pre-imaginal. They were placed in the arena simultaneously, from the same container, and the arenas were inspected at regular intervals until the crickets settled down to rest. Resting was defined as being in the same place for three consecutive observations at intervals of 20 minutes and grouping was defined as being within antennal contact distance of the other cricket.

In an initial series of trials, all resting sites were clean. In a second series, one used resting site (conditioned by either nymphs or adults for at least one week) was offered with nine clean ones. In some of these trials, freshly contaminated substrates were offered , in others, they had been stored at room temperature, in open containers, for varying lengths of time, up to two months.

Results of experiments were tested statistically to find out if they differed significantly from what would be expected if nymphs chose a resting site at random. The expectation of the null hypothesis was that the second nymph to settle would choose a site already containing a nymph by chance in one trial out of ten, since ten sites were offered. The formula used to test this hypothesis was:

$$Z = \frac{X-\frac{n}{k}}{\sqrt{\frac{n(k-1)}{k^2}}}$$

where Z = the value of student's t with infinite degrees of freedom, X = the number of trials in which nymphs grouped, n = total number of trials and k = number of refuges. The null hypothesis is rejected if the value of Z is greater than the table value for the chosen level of significance.

1.3 Results and Discussion

A total of 71 trials were carried out with 10 clean resting sites. Of these, 32 were abandoned, because either only one nymph, or neither nymph, had come to rest during a 12 hour period. In the remaining 39 trials, both nymphs chose a resting site. The null hypothesis predicts that in 39 trials, nymphs would group 3.9 times. The observed number, 12, was significantly larger than expected, at $P < 0.001$.

In 14 trials with one contaminated resting site present, only one nymph did not settle on the used substate. All nymphs settled to rest within 12 hours, and no trials were abandoned. This result was highly significant ($P<0.001$). In many trials, nymphs perched on the used resting site for some interval of time, (a few minutes to several hours), then began moving again, to explore the arena, eat or drink. They always returned to the used resting site. Stored resting sites attracted nymphs as consistently as fresh ones.

1.4 Conclusions

Nymphs of A. domesticus do aggregate spontaneously. They are consistently cued to do this by a substrate previously contaminated by other members of the species, as demonstrated by Sexton and Hess (1968), for adult crickets, but can also form groups in completely clean environments. They are therefore able to respond to cues provided directly by the bodies of other nymphs.

The attractant or arrestant pheromone (or pheromones) deposited by the nymphs is very stable, persisting with apparently undiminished effectiveness for at least two months in the open atmosphere of the laboratory.

These results indicate that nymphs of A. domesticus are very likely to be found resting in groups in natural habitats, and that the groups probably occupy the same locations over long periods of time. These locations presumably will be the most suitable resting sites for members of this species available in the area.

2.0 WHY DO NYMPHS IN GROUPS GROW FASTER THAN THOSE IN ISOLATION?

2.1 Introduction to Section 2.0

In this section I report the results of experiments which I carried out on the proximal causes for faster growth in grouped crickets. I wished to find out if nymphs were really influenced by some attribute of another nymph, or by physical changes in the environment brought about by the presence of other nymphs. If the influence involved another nymph, what differences did its presence make which led to faster growth of its companion? Could a nymph respond to chemical cues only, as it can in choosing a site, or is the presence of another nymph necessary?

2.2 Materials and Methods

2.2.1 Origin and Maintenance of Stocks

Stocks of *Acheta domesticus* (L.) obtained from Laval University and Washington State University were used throughout the project. They were apparently similar in all characteristics. They were kept in glass battery jars or in 128 oz (3.6 litre) pickle jars, which were either left open or partially covered with aluminium foil or plastic film.

Miracle Brand ^{R} Baby Rabbit pellets, previously ground to powder in a kitchen blender, were supplied as food. Water was supplied in straight-sided vials of various sizes, plugged with cotton or rayon batten. Rolled or crumpled paper towelling or Whatman's ^{R} No. 1 filter paper provided resting sites.

Eggs for incubation were laid by females in one ounce (30 ml) plastic cream cups (Lily Brand ^{R}) full of moist sand that were placed in stock jars overnight. They were incubated in the sand in which they were laid, in a tightly closed, screw-topped jar. A piece of moist paper-towelling in the jar maintained high humidity. Eggs of *A. domesticus* hatched in 11-12 days at 31°C, but took longer at lower temperatures.

2.2.2 Rearing Experiments with *Acheta domesticus*

Experiments were incubated at 20°C to 32°C, mostly at 30.5-31.5°C. Temperatures fluctuated no more than ±0.3°C from the one stated. No light was used except where mentioned, and experimental crickets were kept in darkness except when removed from the cabinets for care or manipulation. Dominion Brand ^{R}, one pint (approximately 370 ml), square-sided, wide-mouthed Mason jars, with "Bernardin" snap lids and screw-on metal rings were used for all rearing experiments. I turned the lids upside down to prevent formation of an air-tight seal, and used the white enamel surface thus exposed to record data in wax pencil. The jars were bought in dozen lots in cardboard boxes which were used throughout the project for mass handling. Cardboard partitions within the boxes prevented visual communication between crickets in different jars.

Between experiments, jars were washed with detergent, rinsed, and oven-dried. Rings and lids were air-dried, since they tended to deform at higher temperatures.

Each jar used in an experiment was furnished with a one dram vial of water plugged with rayon or cotton, a 13 cm x 5 cm strip of Whatman's ^{R} No. 1 filter paper, rolled lengthwise into a scroll, and about 5 ml of ground rabbit diet in a loose pile in one corner. In experiments on food intake, ground diet was sieved at 20 mesh, mixed with 0.4% agar solution and dried at 50°C, to form cakes. Fragments of cake were easy to separate from faeces because of their much lighter colour. Experiments were set up as randomized block designs, to distribute treatments throughout the boxes. Treatments were randomly arranged within blocks after the jars had been fully prepared and nymphs were assigned to treatments by filling jars sequentially.

Nymphs from the same hatch were used for all treatments. The period over which they hatched ranged from four to 24 hours. Before being assigned to treatments they were all held together in the hatching jar for 12-24 hours after the egg tub had been removed.

Water vials were usually replaced on or around the 14th day after the experiment began,and again usually around the 24th day, when more food was also supplied. After this, care became more individualized because the larger nymphs sometimes polluted their water source or pulled out the cotton plug and flooded their jar.

When nymphs were weighed during an experiment, they were tipped or shaken from their rearing jar into a plastic vial of known weight, without anaesthetic, and tipped back into the jar afterwards. All weighings were done within as short a time as possible.

2.2.3 Experiments with Gryllus Species

One female of G. veletis (Alexander and Bigelow) and two females of G. fultoni were collected in June 1975 in southern Indiana. All laid several hundred eggs in captivity, and survived well on the same diet as given to A. domesticus stocks. Eggs of G. veletis hatched in about 12 days at 31°C, and those of G. fultoni in about 13 days. First instar nymphs of Gryllus spp. survived in much higher numbers if humidity in the rearing containers was high, but later instars tolerated low humidity well.

In order to carry out successful experiments with North American field crickets, I had to increase humidity in the experimental jars, at the beginning of each experiment. I covered the floor of each jar with a 6.5 cm x 6.5 cm square of filter paper moistened with 0.6 ml of distilled water before putting nymphs into the jars. The paper was remoistened 2 days later with 0.4 ml of water. After this the jars were allowed to revert to ambient humidity. The nymphs had, by that time, become more hardy and high mortality was avoided All nymphs in the experiment received this treatment. All other experimental procedures were the same as in other studies on A. domesticus.

2.2.4 Analysis of Results

The results of rearing experiments were analysed by parametric methods. Analysis of variance was used when several treatments were involved, followed by Duncan's New Multiple Range Test. When only two treatments had to be compared, either analysis of variance or Student's unpaired t-tests were used.

Although experiments were always set up as randomized block designs they were analyzed as being completely randomized, because deaths during the course of the experiments usually reduced the number of complete blocks substantially.

2.3 Is Faster Growth in Grouped Nymphs a Mass Effect?

2.3.1 Introduction to 2.3

Since all experiments, both in this study and in those reported in the literature, have been carried out in small closed containers, it seemed possible that increased growth rate in grouped nymphs might be due to an increase in temperature, humidity or some other factor in jars, related to the number of nymphs in them. If this were true, it would mean that the acceleration of growth rate might be an artifact of experimental design, not found in less protected natural environments. Thus the phenomenon might have little meaning in the life of the insect. Chauvin's (1958) containers were too small to allow complete, normal development of nymphs to adults. He found nymphs in these containers grew fastest in groups of three. McFarlane (1964) reported an increase in growth rate with increase in group size from five to ten. Charpentier et al., (1972) reported no difference between groups of two and groups of six, but in their axenic conditions growth rate was severely retarded anyway. Thus it is not clear from the literature if growth rate is related to density.

I carried out direct measurements of temperature and humidity. Rearing experiments with groups of differing density were also carried out, since changes might be subtle, or involve some other parameter.

2.3.2 Direct Measurements

Direct measurement of temperature and humidity within jars was made using a Yellow Springs Instruments Telethermometer and a Dew Point Hygrometer (model 91HC) from the same company. Temperature measurements made within a standardly furnished rearing jar were compared with measurements made in the cabinet. The two probes were shown to record identically before the tests began. The probe was suspended in the air inside the jar, after passing through a rubber ring in the jar lid. Measurements were made in an empty jar and with one, two, three and four last instar nymphs in the jar. The temperature within the jar corresponded to the temperature in the cabinet to within 0.1°C and did not vary with the number of crickets placed in the jar.

Measurement of humidity was more difficult. The machine could give only one reading at a time, which was consistent to 1.5% RH over saturated salt solutions. It required at least two hours to adjust to a constant reading in a given humidity. The recording probe generated heat which, in still air in a confined space, gradually altered the instrument's readings and made it appear that humidity had declined. If the machine was not left running continuously during tests, the probes had to be oven-dried to prevent damage on reconnection.

In order to make conditions in the jar as stable as possible, it was placed in a desiccator over calcium chloride solution, which maintained 35% RH in the closed container. The desiccator lid was replaced by a sheet of Plexiglas, drilled to fit a rubber bung through which the recording probes were inserted. The lid of the jar was within three millimetres of the underside of the Plexiglas and was similarly drilled to fit the bung. Thus the probes could be inserted into the jar rapidly, with as little disturbance as possible to the atmosphere inside. A solid rubber bung of identical size was fitted into the same position before a test, when the probes were not in position.

To take a reading, the probes were inserted into the jar in the desiccator and left in position for three hours. Readings were taken, then the probes were removed and the solid bung replaced. The procedure was repeated after several hours. Readings were taken with no crickets in the jar, and with one, two, three and four last instar nymphs. Twenty-four hours elapsed between the time an extra nymph was placed in the jar and the time testing began.

Humidity in the jar varied with the condition of the water vial but evaporation from this source was found to remain constant over a period of about ten days, in the constant humidity conditions of the desiccator. Relative humidity was about 41.50 to 43.10%, and was not increased by the addition of pre-imaginal nymphs to the jar.

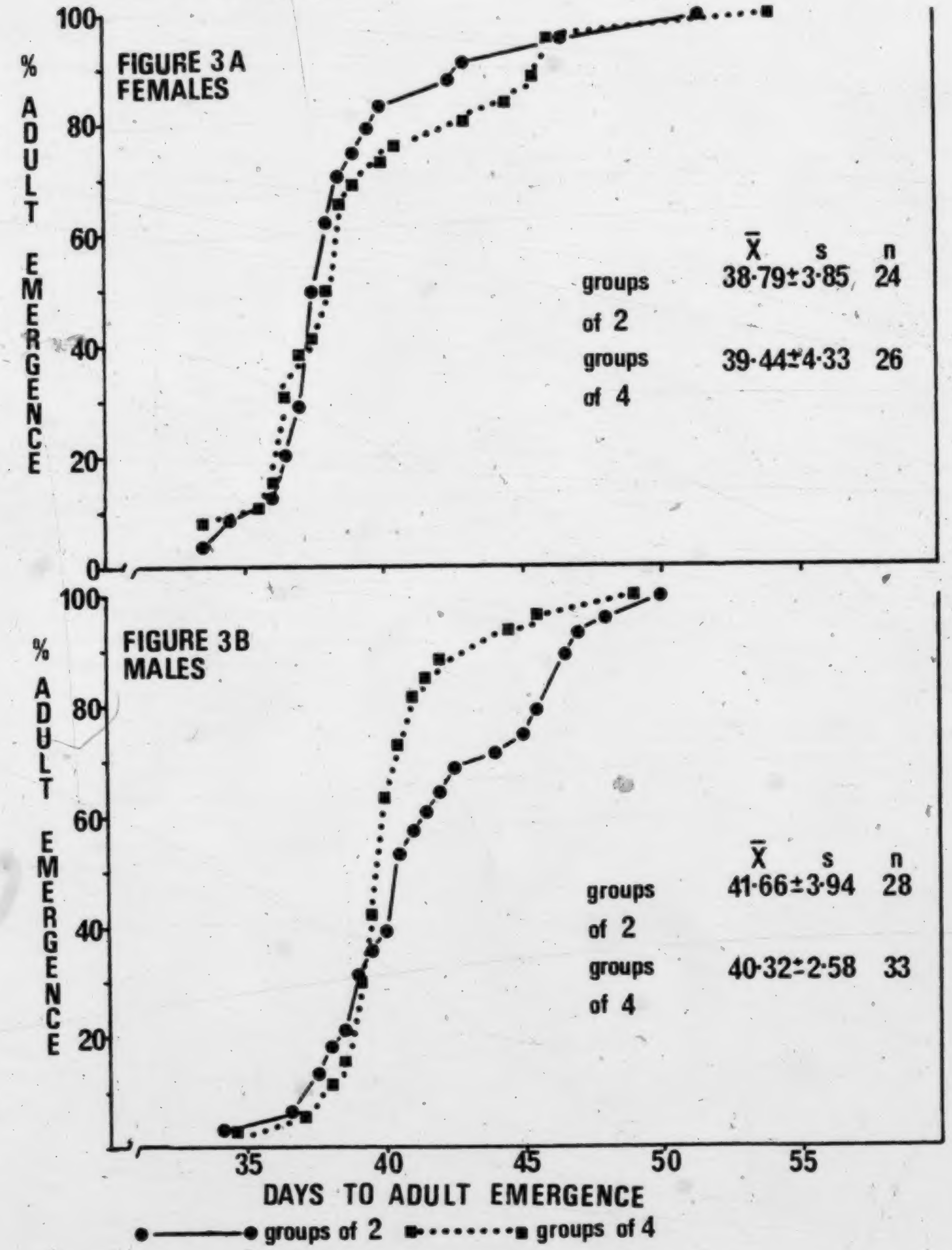
Since the nymphs used were nearly full-grown, weighing more than 300 mg each, it was more likely that they would produce a measurable effect on the atmosphere of the jar than would first instar nymphs weighing less than one milligram each. Thus these results demonstrated that nymphs did not produce any change in temperature or relative humidity detectable by the instruments used. If any change occurred, it must have been very local, and incapable of affecting the whole atmosphere inside the jar, even over a period of several days equilibration.

2.3.3 Experiments 1 and 2

2.3.3.1 Procedure: Two rearing experiments were performed using slightly different designs and procedure. In Experiment 1, two treatments only were used, which were groups of two and groups of four with 80 nymphs in each treatment. They were weighed within 24 hours of emerging as adults. Experiment 2 had three treatments, groups of two and four and isolated nymphs, with 55 in each treatment. These nymphs were weighed 30 days after hatching, but not at adult emergence. Experiment 1 was incubated at 30.5°C and experiment 2 at 31.5°C.

2.3.3.2 Results and Discussion: Experiment 1 showed no significant difference between treatments either in developmental period (fig. 3) or in weights at emergence (Table 1) in either sex.

Fig. 3. Cumulative adult emergence (days) in Experiment 1, on effect of group density on development.



There are no significant differences except between sexes

Table 1

Experiment 1, mean weights in mg of crickets at adult emergence (± standard deviation).

Treatment	Males	Females
Pairs		
	351.29±63.03	382.73±49.02
sample size	25	23
Groups of 4		
	368.73±36.10	396.45±52.82
sample size	27	24

Experiment 2 showed highly significant differences in weight between isolated and grouped nymphs at 30 days (P<0.01) and in developmental period (P<0.01((Table 2, fig. 4), and no significant difference between the two grouped treatments.

In both experiments (figs. 3B and 4B), males in denser groups tended to mature slightly faster than those in pairs, although the difference was not great enough to be significant (P<0.05). These results agree with those of McFarlane (1964) since inspection of his tables shows that it was only males which grew faster in groups of 10 than in groups of 5 in his experiments. The results which he presented for females resemble my own results from Experiment 1.

Jobin and Huot (1966), using groups of 25, found the same sort of difference between growth rates of males and females as occurred in my experiments, so that it does not appear that male growth rate gradually increased as group size increased. Male growth rate remained slower than female even in large groups.

The fact that there was no major difference in growth rate between nymphs in pairs and those in groups of four implies that the density of the larger group did not produce overcrowding phenomena in nymphs up to the time of adult emergence.

Clearly, differences between grouped and isolated

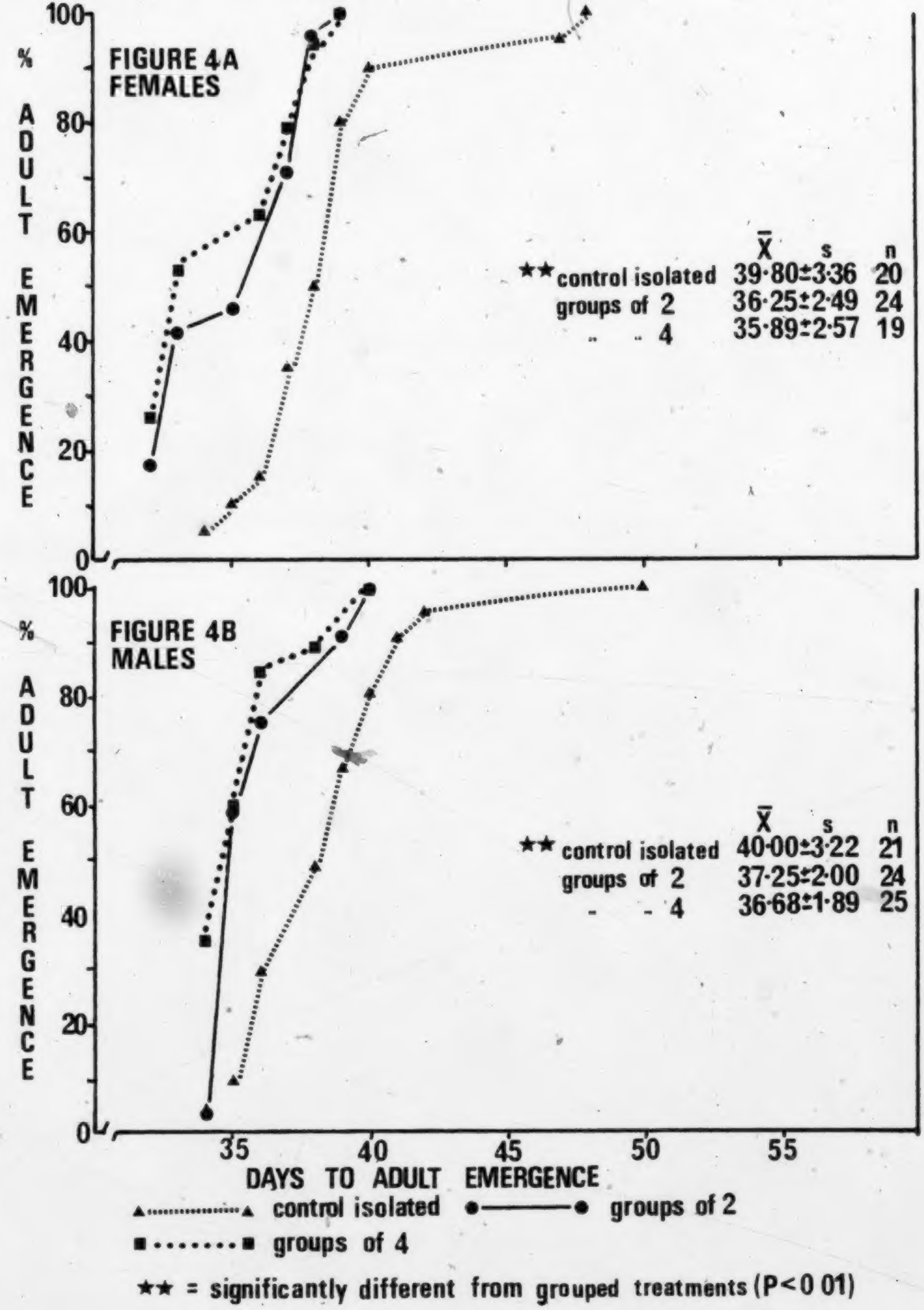
Table 2

Experiment 2, mean weights in mg of crickets at 30 days (± standard deviation).

Treatment		
Pairs	Males	Females
	313.05±42.07	354.91±79.70
sample size	26	22
Groups of 4		
	326.32±49.73	356.43±77.03
sample size	25	19
Isolated		
	250.37±58.76**	243.84±80.57**
sample size	21	20

** = significantly lighter than nymphs in grouped treatments ($P<0.01$).

Fig. 4. Cumulative adult emergence (days) in Experiment 2, on effect of group density on development.



crickets cannot be attributed to differences in temperature, humidity or any other factor produced by the insects themselves in their own enclosed environment.

2.3.4 Summary

1) Temperature and relative humidity in rearing jars were not measurably affected by the presence of up to four penultimate instar nymphs.

2) There was no significant difference in growth rate between nymphs in groups of four and those in pairs, but males in larger groups tended to mature slightly faster than those in pairs.

3) Isolated nymphs were significantly lighter than grouped ones at 30 days, and emerged as adults significantly later.

2.4 Is Food Intake and Use Different in Grouped and Isolated Nymphs?

2.4.1 Introduction to Experiment 3

Several studies have been done on food consumption and growth in A. domesticus at various life stages; for example, Crossley and Van Hook (1970) on adult males, Lipsitz and McFarlane (1971) on nymphs throughout growth, Woodring, Roe and Clifford (1977) on female nymphs in the last two instars, and Patton (1978) on the whole of nymphal life and early adulthood. However, none have been concerned with differences associated with grouping and isolation. This influence has been considered in adult males of Schistocerca gregaria (Norris, 1961), which digest food more efficiently if in groups.

If grouped nymphs grow faster than isolated ones, they obviously must turn food into body tissue at a faster rate. This may result from their eating more food, or from some difference with regard to how food consumed is used, or a combination of both. I carried out an investigation of food consumption and use in grouped and isolated nymphs to try to find out how growth rate is determined.

2.4.2 Procedure in Experiment 3

Experiment 3 compared food consumption and use in grouped and isolated nymphs during the fifth and sixth instars of nymphal development. It was decided to use two complete instars because food consumption and faeces production change daily during the course of an instar (Woodring, Roe and Clifford, 1977). Measurements of weight gained, food eaten and faeces passed may be compared more meaningfully if they represent the same life-cycle interval in all individuals studied. The fifth and sixth instars **were chosen** because by the beginning of the fifth instar the amounts of food consumed and faeces produced within one instar are large enough that differences between treatments would not be obscured by lack of accuracy of measurement. This period also falls within the exponential part of the growth curve during which growth rate is fastest, and which is therefore most suitable for short term nutrition studies (Patton, 1978).

Nymphs were reared in groups or in isolation until just before the moult to fifth instar when the gut was empty. At this stage they and their food supply for the following two instars were weighed. **Nymphs**, remaining food and faeces were weighed at the end of the fifth and sixth instars. Food was found to absorb a predictable proportion of water, which was subtracted before calculations were performed. It was not possible to measure individual food intake or faeces production of grouped nymphs, so that only average values for each member of a group in a jar were obtainable. Nymphs were grouped with others of similar weight at the beginning of the experiment.

The weights of food and faeces, with the mean weights of nymphs calculated by integration under the growth curve, were used to calculate five ratios: consumption index (CI) (= grams of food eaten/gram body weight/day) relative growth rate (GR) (= grams of weight gained/gram body weight/day), efficiency of conversion of ingested food to body substance (ECI) (= GR/CI), approximate digestibility of food (AD) (= percentage of ingested food which is converted to body substance) and efficiency of conversion of digested food) (ECD) (= weight gained/weight of food ingested) (Waldbauer, 1968). These ratios were calculated for each jar in the experiment and the results analyzed by means of unpaired t-tests.

2.4.3 Results and Discussion

The results of the study are shown in Table 3. Grouped nymphs were heavier than isolated ones at the end of the fourth instar ($P<0.001$), and reached that stage significantly faster ($P<0.001$). These differences persisted and increased during the period of the study, so that grouped nymphs took a shorter period to complete the fifth and sixth instars ($P<0.05$) and were still heavier at the end ($P<0.001$). In keeping with these differences, grouped nymphs ate more food than isolated ones during this period ($P<0.01$).

As table 3 shows, CI GR and ECl were all significantly higher in grouped nymphs. There was no significant

Table 3

Experiment 3. Study of food consumption and use in fifth and sixth instars of *A. domesticus*.

	Days from hatching to start of 5th instar	Mean Wt (mg) at moult to 5th instar	Dur-tion of 5th & 6th instars (days)	Mean Wt (mg) at moult to 7th instar	Food Faten (mg)	CI	GR	ECI	AD	ECD
grouped	30.10	20.92	15.31	75.64	86.154	0.101	0.062	61.91	46.59	131.00
n=41 individuals	±1.88	±4.60	±0.31	±21.63	±28.053	±.012	±.008	±5.72	±2.93	±13.15
17 groups										
isolated	31.64	16.69	15.91	53.03	61.81	0.092	0.054	57.04	47.55	123.34
n = 45	±1.98	±3.78	±1.68	±15.35	±19.90	±.019	±.012	±10.77	±2.49	±19.40
t value	3.74	4.65	3.32	5.74	3.20	2.26	3.09	2.26	0.96	1.72
significance	***	***	*	***	**	*	**	*	-	-

Mean weights are given with standard deviations

* = $P<0.05$ ** = $P<0.01$ *** = $P<0.001$.

difference in AD between treatments, nor in ECD, though this was higher in grouped nymphs.

Thus, grouped nymphs ingested more food per milligram of body weight and converted it to body tissue more efficiently over the period of the study, regardless of their initial weight.

It thus appears that grouping nymphs together both stimulates them to feed more, and increases the proportion of food consumed which becomes body tissue.

Improvement in ECI in grouped crickets implies that the presence of other nymphs improves some aspect of their physiological efficiency. What this might be cannot be judged from this study.

2.4.4 Summary

1) Grouped nymphs consumed more food per milligram of body weight and converted it to body tissue more efficiently than did isolated nymphs, during the fifth and sixth instars.

2) Grouped nymphs completed these instars, and those preceding the start of the experiment, faster than did isolated nymphs.

2.5 How is Weight Gain Related to Number and Duration of Instars in Grouped and Isolated Nymphs?

2.5.1 Introduction to 2.5

The number of instars through which members of the Orthoptera pass before becoming adult is known to vary, and crowded nymphs of *S. gregaria*, *Nomadacris septemfasciata* (Serv.) and *Anacridium aegyptium* (L.) all have fewer instars than isolated ones (Uvarov, 1966, citing several authors).

Ghouri and McFarlane (1958) reported that nymphs of *A. domesticus*, reared in groups of 10, went through 7 or 8 nymphal instars before emerging as adults, at 28°C, and through 8 or 9 instars at 35°C, although at the higher temperature, development was faster. Females developed faster than males, and the last two nymphal instars were longer than the earlier ones.

Jobin and Huot (1966), using subjects from the same stock, reared nymphs in groups of 25, and recorded 9 or 10 instars at 35°C. Their other observations supported the findings of Ghouri and McFarlane (1958). Those nymphs which had an extra moult had a longer developmental period than those which did not. In their experiment, about 61% of males and 57% of females had 9 nymphal instars.

As an adjunct to the feeding study (Experiment 3), I collected data on the relationship between number of instars and growth rate in grouped and isolated nymphs.

2.5.2 Results from Experiment 3, and Discussion

The nymphs in Experiment 3 were known to have undergone four instars before the feeding study started, and all moulted to the seventh instar at the end of the study. Of the grouped nymphs, 12 (28%) had wing-pads after this moult, which always marks the beginning of the last two nymphal instars, and would have had a total of 10 instars, counting the imago. The development of the nymphs was followed long enough to determine when they developed wing-pads. Twenty-four (58%) would have had 11 instars and 5 (14%) would have had 12. Of the isolated nymphs none would have had 10 instars, 22 (48%) would have had 11, 22 (45.4%) 12 and 3 (6.5%) 13 instars.

All nymphs achieved a weight of at least 96 mg before the moult after which wing-pads appeared. The mean weight of nymphs which developed wing-pads in the seventh instar was 106.35± 7.63 mg; in the eighth instar, 123.74± 11.03 mg; in grouped nymphs 126.57± 17.82 mg in isolated ones; and in the ninth, 144.27± 28.71 mg (selected representative sub-samples of isolated nymphs only, the rest having been killed).

Williams, (1976) quotes Nijhout's work on larvae of Manduca sexta (Johannson) (Lepidoptera, Sphingidae) (1975) showing that if larvae were starved in early instars, making them smaller than usual when they moulted to the 5th instar, they did not pupate, as they would normally have done, unless the head capsule exceeded a certain size. If it was smaller, they underwent another larval instar. As Williams (1976) quotes Sehnal:

> Apparently an insect does not 'count moults' before pupation. Rather it 'measures' its growth rate and when this growth rate is maximal under the conditions of nutrition that exist, it turns off its corpora allata and pupates.

My results using A. domesticus nymphs conform to this hypothesis, although this study dealt with a hemimetabolous insect.

A nymph underwent another instar even if it missed the critical weight by only a few milligrams. Such nymphs were far over the threshold weight when they next moulted, which accounts for the higher mean weights of nymphs acquiring wing-pads at later moults.

However, the variation in weight at the moult was considerable, and there is not usually any significant difference between grouped and isolated nymphs in weights at emergence, despite the fact that isolated nymphs have often undergone one or more extra instars.

2.5.3 Summary

1) Grouped nymphs tended to have one or more fewer instars than did isolated nymphs.

2) Nymphs did not develop wing-pads until they weighed a minimum of 96 mg.

2.6 Do Isolated Nymphs Grow Faster When in Contact With Substrates Contaminated by Other Crickets?

2.6.1 Introduction to 2.6

Growth rate is affected by pheromones in locusts and cockroaches (Brossut, 1975). McFarlane's results (1966 a,b,c, 1967, 1968) indicated that methyl laurate and methyl linolenate presented on substrates, could increase growth rate or weight at maturation in isolated nymphs of A. domesticus. Methyl linolenate presented on filter paper caused loss of tarsal segments of newly hatched nymphs, after the first initial moult (McFarlane, 1972), which was interpreted as evidence that this chemical was absorbed through the tarsi directly.

Results reported in Section 1.0 show that nymphs of all ages were attracted to substrates previously used by other crickets, which indicates that they can probably recognize chemicals deposited there. It therefore seemed likely that such chemicals might affect growth rate as well as inducing aggregation.

McFarlane (1978) reared isolated nymphs in jars previously used by groups of nymphs, so that the isolated nymphs were exposed to used substrates and faeces produced by larger crickets. Growth rate was slower in these isolated nymphs than in grouped nymphs in uncontaminated jars. McFarlane concluded that no accelerating compound was contained in waste products.

In an experiment of similar design, but in which most faecal pellets were removed from the jars, I found similar retardation, associated with higher first instar mortality. The contaminated substrates from these jars retained their ability to attract nymphs in arenas three weeks after the experiment was concluded. Thus neither McFarlane's published results, nor those of my own experiment using his method showed any positive effect on growth rate of exposure to the chemicals either contained in faeces or deposited on substrates by other crickets.

It seemed possible that bacterial contamination or toxins from faeces could be masking positive effects of attractive chemicals Since effects sometimes change with concentration of chemical (e.g. alarm pheromone of Atta texana, Moser, Brownlee and Silverstein, 1968), a high concentration of attractant could be exerting a repellent effect.

Thus I investigated the effect of providing isolated nymphs with concentrations of whatever chemicals are deposited onto substrates by grouped nymphs similar to those which grouped nymphs would encounter and of gradually increasing the concentration during development. This was accomplished by using grouped nymphs of the same age as the experimental isolated nymphs to contaminate the substrates and exchanging these substrates frequently.

2.6.2 Procedure in Experiments 4 and 5

In both experiments, paper resting scrolls were exchanged between isolated and grouped nymphs, every second day during development. In order to provide more used substrate, water vials were also exchanged in Experiment 4, and in Experiment 5, aluminium foil dishes containing food were exchanged, but not water vials. Isolated control nymphs were subjected to a sham transfer operation in which their own scroll and water vial (or food dish) was removed from the jar and immediately returned. This was necessary because a preliminary experiment had indicated that any handling reduces growth rate in nymphs, a phenomenon also found by Woodring, Clifford, Roe and Beckman (1978). In Experiment 4, (30.5°C, no light cycle) groups were of six nymphs, and the original sample size of isolated treatments was 42. In Experiment 4 (29°C:, LD 12:12), groups were of 3 nymphs, and sample size of isolated treatments was 60. Nymphs in Experiment 5 were weighed at 42-44 days.

2.6.3 Results of Experiments 4 and 5, and Discussion

Mortality in Experiment 4 was 29%. Losses included deaths, mostly in the first instar, during the first 3 days, and escapes. If both experimentals in a block died, during the first instar, I substituted one isolated control as an experimental. Five such substitutions were made. At the end of the experiment the average number in groups was 4.4.

Cumulative emergence curves (fig. 5) show that the means for experimentals lie between those of grouped nymphs and isolated controls. However, they did not differ significantly from the isolated controls ($P<0.05$). Nymphs in groups developed significantly faster ($P<0.01$) than those in either isolated treatment. Since sample sizes in isolated treatments were reduced by mortality, Experiment 5 was performed.

As in Experiment 4, grouped female nymphs grew significantly faster than isolated ones ($P<0.01$), (Table 4 and fig. 6). Experimental females grew at an intermediate rate, insignificantly different from either of the other treatments ($P<0.05$).

Males did not show significant differences between control treatments, either in weight at 42-44 days, (Table 6) or in developmental period (fig. 5B). (Sample size is smaller in the grouped treatment at 42-44 days than at emergence, because 3 groups were overlooked during weighing, and their weights were not recorded). Males in the experimental treatment were significantly slower to mature than those in groups ($P<0.05$).

In neither of these two experiments did male nymphs show any faster growth when provided with contaminated substrates. The fact that isolated male nymphs grew no slower than grouped ones in Experiment 3 renders the results for

Fig. 5. Cumulative adult emergence (days) in Experiment 4, on effect of contact chemical stimulation on development, substrates exchanged between groups and isolated individuals (= experimentals).

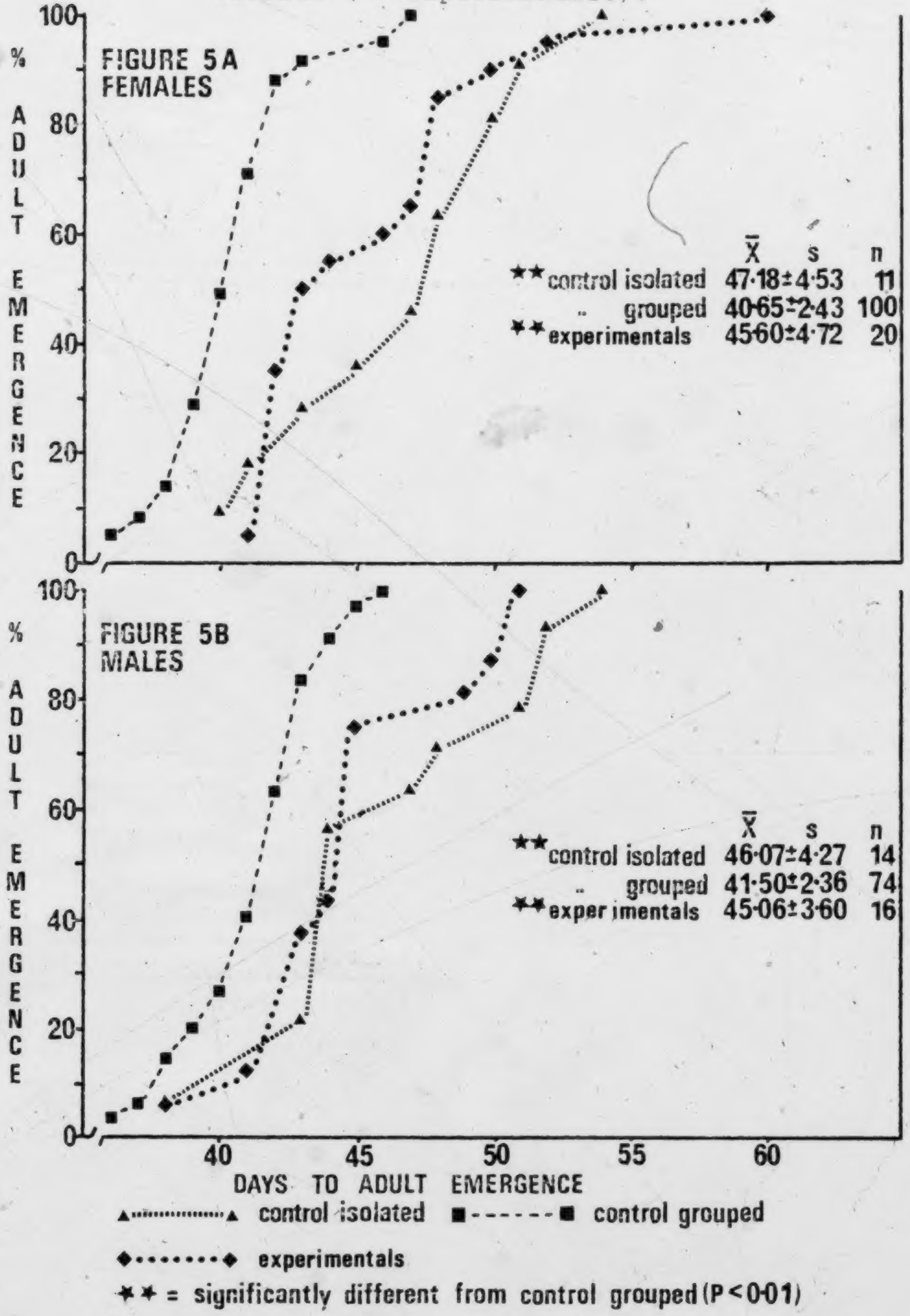


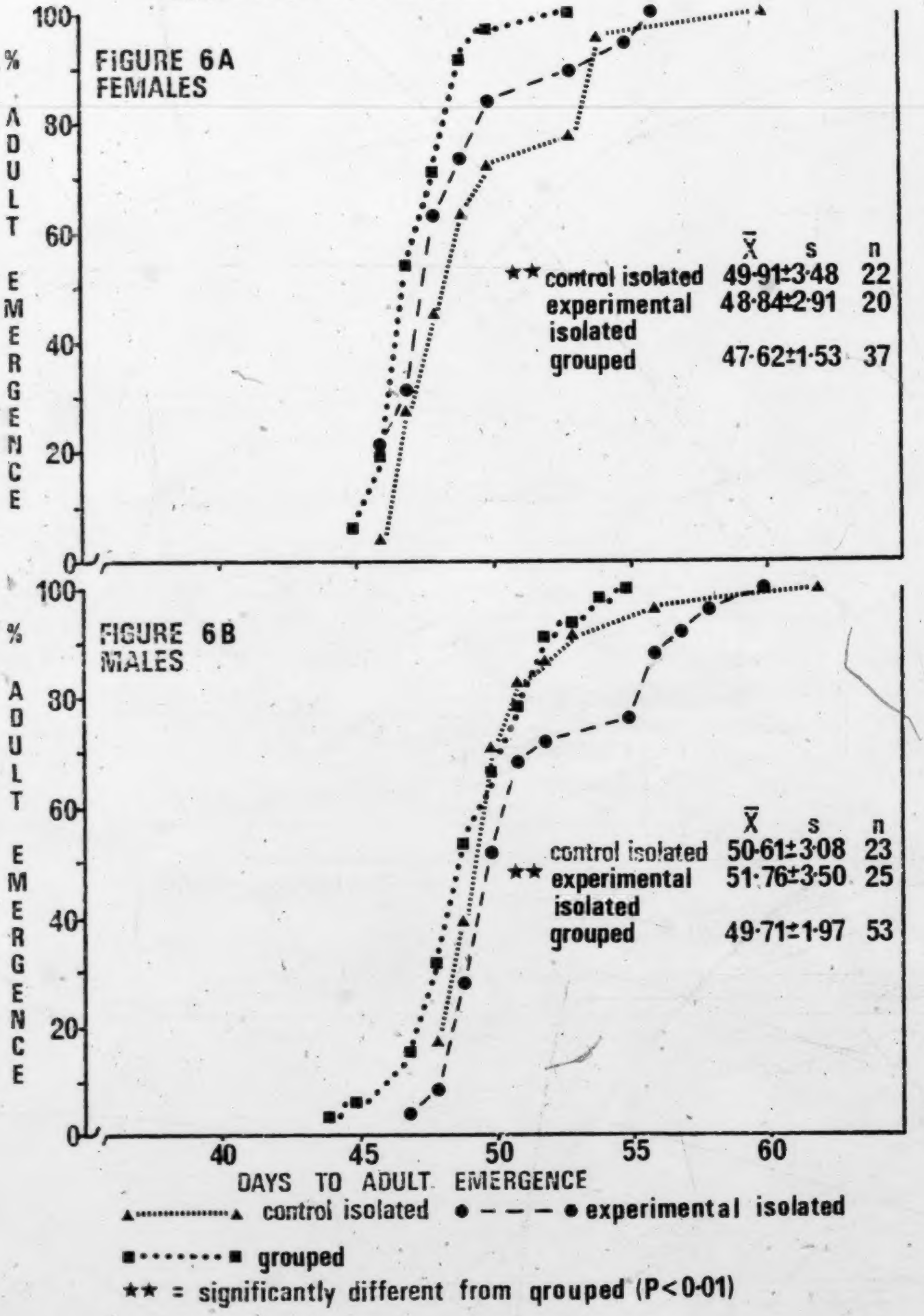
Table 4

Experiment 5, mean weights in mg at 42-44 days (± standard deviation).

	Isolated Controls	Isolated Experimentals	Groups
Males			
	344.89±101.44	338.71±96.40	359.16±77.87
sample size	23	26	44
Females	348.70±100.69**	379.74±86.77	419.29±67.43
sample size	23	19	37

**= significantly lighter than subjects of the same sex in grouped controls ($P<0.01$).

Fig. 6. Cumulative adult emergence (days) in Experiment 5, on effect of contact chemical stimulation on development, substrates exchanged between groups and experimantal isolated individuals.



nymphs with exchanged substrates more convincing. Female nymphs with contaminated substrates, grew slightly faster than isolated controls, but did not achieve the same growth rates as grouped nymphs. It seems possible that females grew faster in response to chemical cues, but clearly, if this was so, they did not receive an adequate dosage of the chemical involved to make the difference significant.

2.6.4 Summary

1) Only female nymphs showed any tendency to grow faster when exposed to recently contaminated substrates. They did not grow significantly faster than females on clean substrates. Male nymphs showed no faster growth rate than isolated males and in one experiment were significantly slower.

2.7 Can the Presence of Members of Other Species Affect Growth Rate in Nymphs of *A. domesticus*?

2.7.1 Introduction to 2.7

In some species of insects showing 'grouping effects', there is evidence that the phenomena can be induced by the presence of members of other species. Izutzu, et al., (1970) reported that nymphs of *Blattella germanica* (Dictyoptera, Blattellidae), which grew faster when grouped with others of their own species, also grew faster when grouped with nymphs of *Periplaneta americana* (L.), *P. fuliginosa* (Serville), and *P. japonica* (Karny) (Blattellidae), or even with those of *Homoeogryllus japonicus* (de Haan) (Gryllidae). Evidence from several experiments indicated that they responded to tactile stimulation, using their antennae to transmit and receive it, and did not require any pheromone to influence growth.

Levita (1962) reported that nymphs of *G. bimaculatus* which are lighter in colour in groups than in isolation, responded in the same way to contact with nymphs of *G. campestris*, *G. capitatus* (Saussure) and *G. assimilis* (Fabricius), but not with those of *G. posticus* (Walker).

McFarlane (1964) found that in groups comprising 5 nymphs of *A. domesticus* and 5 of *Gryllodes sigillatus* (Gryllidae), *A. domesticus* nymphs developed faster than when reared singly, but he did not try rearing single nymphs of both species together.

I reared single nymphs of A. domesticus with nymphs of Gryllus species.

2.7.2 Procedure in Experiments 6 and 7

In Experiment 6 nymphs of G. veletis were used, and in experiment 7, those of G. fultoni. These nymphs were F2 from the females discussed in 2.2. Experiment 6 had both grouped and isolated nymphs of A. domesticus as control treatments, but Experiment 7 had only grouped ones. In both experiments one A. domesticus nymph was grouped with two Gryllus nymphs and control A. domesticus groups were of three nymphs. There were about 60 A. domesticus nymphs in each treatment in both experiments, which were weighed towards the end of nymphal development. Gryllus nymphs were not weighed, nor were they kept in rearing jars to complete development after nymphs of A. domesticus had emerged as adults. This was because nymphs of G. veletis and G. fultoni, with few exceptions, spend several weeks in the last three nymphal instars which prolongs their developmental period to three months or more.

2.7.3 Results of Experiments 6 and 7, and Discussion

Weight data (Table 5) and maturation rates (fig. 7) from experiment 6, show that A. domesticus nymphs of both sexes in control groups matured faster ($P<0.01$) than isolated

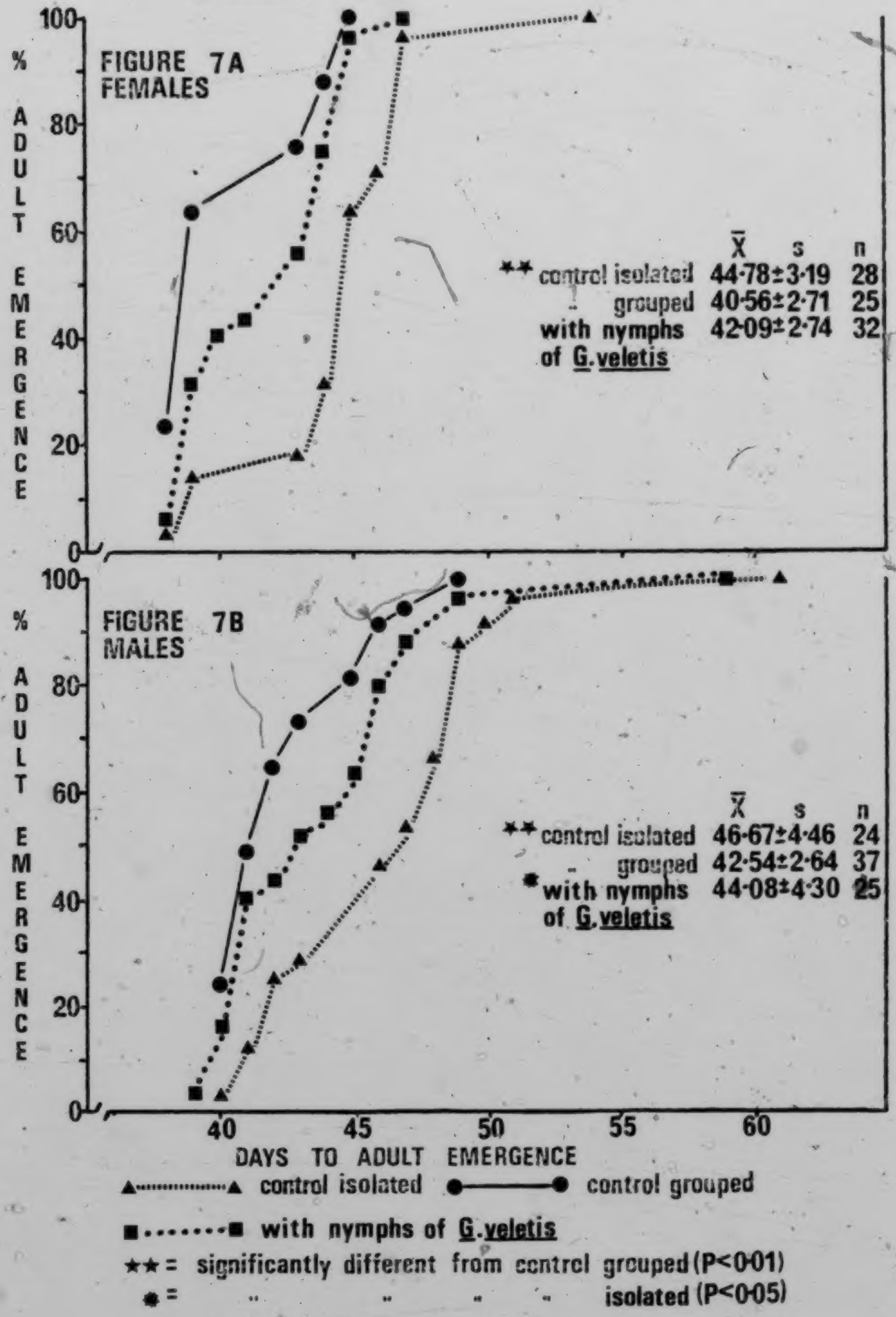
Table 5

Experiment 6, mean weights in mg at 36 days (± standard deviation) (excluding nymphs without wing-pads).

	Isolated	Grouped with other *A. domesticus* nymphs	Grouped with nymphs of *G. veletis*
Males	282.80±71.64**	355.60±71.28	338.36±94.98
sample size	22	40	22
Females	272.00±66.80**	376.00±84.20	349.47±68.55
sample size	28	26	34

** = significantly lighter than subjects of same sex in other treatments ($P<0.01$).

Fig. 7. Cumulative adult emergence (days) in Experiment 6, on development of nymphs of A. domesticus grouped with those of Gryllus veletis.



nymphs. Those grouped with nymphs of G. veletis gained weight ($P<0.01$) and emerged as adults significantly sooner than isolated nymphs ($P<0.01$ in females, $P<0.05$ in males). Growth rates of nymphs grouped with G. veletis nymphs did not differ significantly from those of grouped controls.

The characteristics of the experimental sample, however, were not identical with those of the grouped control sample. The mean weight of nymphs of both sexes was lower (Table 5), and the mean developmental period longer (fig. 7). Histograms of emergence showed two clearly separated peaks in all samples. Whereas in peer groups 64% of females and 72% of males were included in the earlier peak, the corresponding values for nymphs with G. veletis nymphs were 44% and 52% (fig. 8).

Thus, while A. domesticus nymphs reared with nymphs of G. veletis certainly grew significantly faster than those reared in isolation, they apparently did not completely duplicate the growth rate of those reared with nymphs of the same species.

Weight data (Table 6) and maturation rates (fig. 9) from Experiment 7, both show that there was no significant difference between treatments, either in males or females. The results for both treatments were so similar that they might represent one sample only. The difference between developmental rates in males and females was almost identical in both treatments.

Fig. 8. Experiment 6, Adult emergence by days.

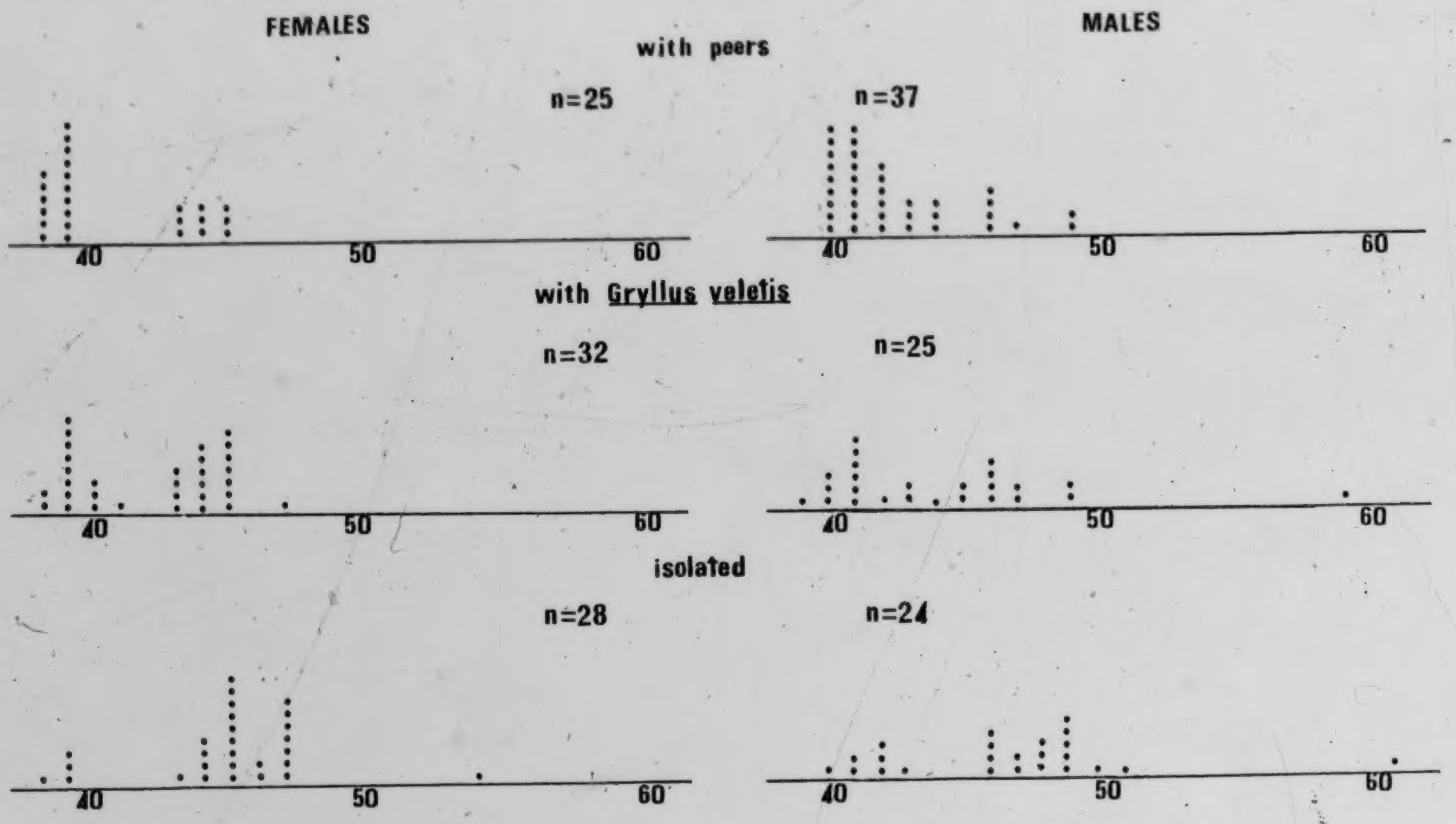


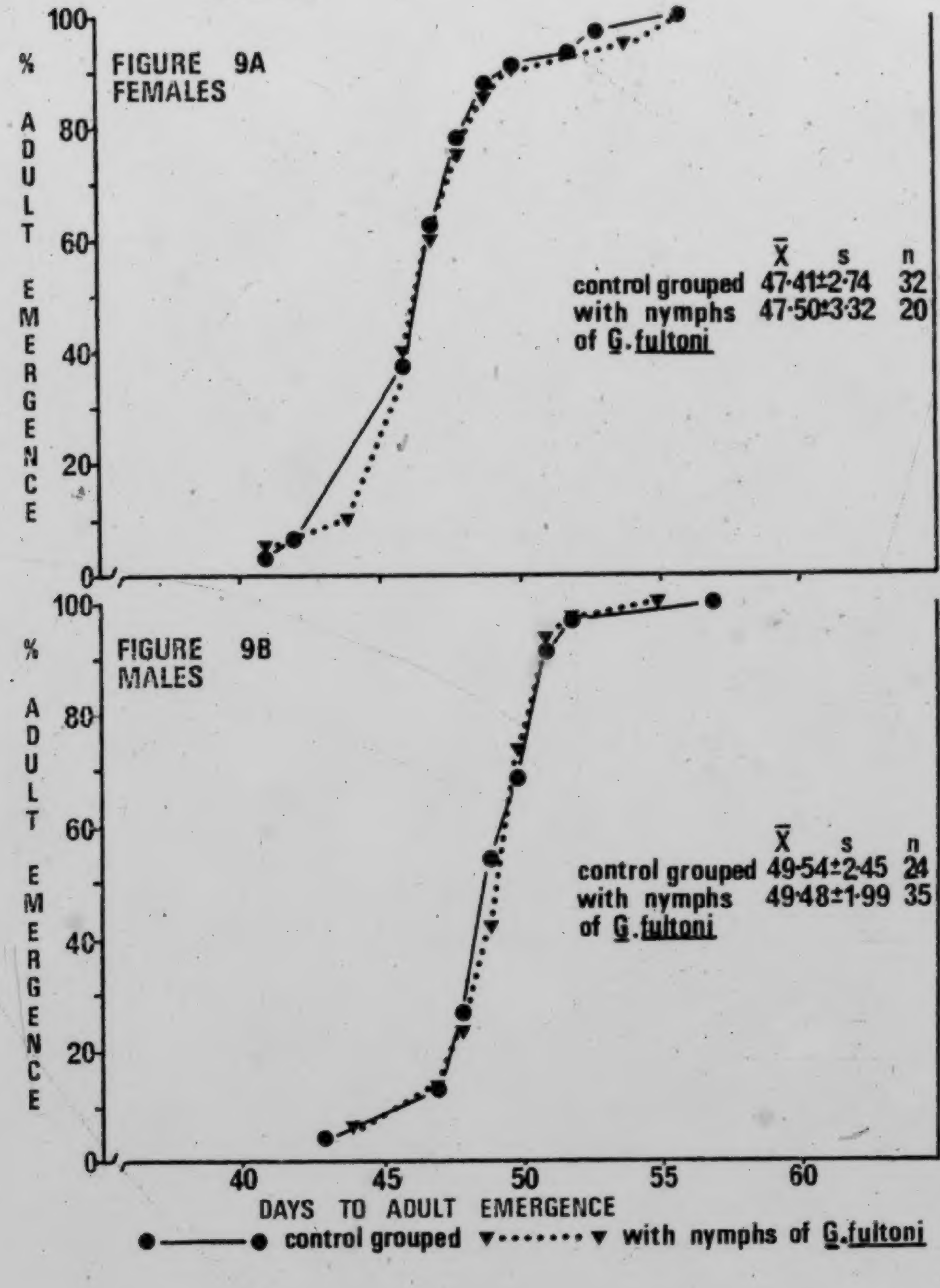
Table 6

Experiment 7, mean weights in mg at 42-44 days (± standard deviation).

	Grouped with other nymphs of *A. domesticus*	Grouped with nymphs of *G. fultoni*
Males	414.05±51.36	405.30±76.65
sample size	20	31
Females	427.88±81.05	446.89±93.77
sample size	34	19

There are no significant differences between subjects of the same sex in different treatments, at $P<.05$.

Fig. 9. Cumulative adult emergence (days) in Experiment 7, on development of nymphs of *A. domesticus* grouped with those of *Gryllus fultoni*.



Thus, the effect of grouping a nymph of A. domesticus with 2 nymphs of G. fultoni appears to be exactly the same as grouping it with 2 other nymphs of its own species.

The difference in results between the two experiments may be related either to differences between G. fultoni and and G. veletis, or to differences in regime between the two experiments. I consider it more likely that they are due to differences between the two species, since the only major difference in regime was the light cycle in the second experiment. G. veletis adults are slightly larger than those of G. fultoni and males are more aggressive and territorial. The behavior of nymphs of either species has never been investigated, but nymphs from neither of these two stocks grew faster in groups (see Section 3.8).

The results of both experiments show that, as in G. bimaculatus nymphs, and in those of Blattella germanica, stimuli which optimize the growth rate of nymphs of A. domesticus are not species specific.

2.7.4 Summary

1) Nymphs of A. domesticus grew as fast when grouped with nymphs of G. fultoni as they did when grouped with nymphs of their own species.

2) They grew nearly as fast when grouped with nymphs of G. veletis but the mean developmental period was slightly

longer, in both sexes.

2.8 Does Maternal Age Affect Growth Rate of Nymphs?

2.8.1 Introduction to 2.8

Although re-analysis of Chauvin's (1958) data shows that differences in growth rate between grouped and isolated nymphs were significant both when parents were young and when they were old, the data do show that the difference between treatment means was much greater in the offspring of old parents. Grouped nymphs weighed 130.65 ± 27.49 mg at 30 days, while isolated ones weighed 29.35 ± 17.42 mg (n=23 in both samples). The corresponding values for the offspring of young parents were 46.57± 15.34 mg (n=23) and 21.96± 12.62 (n=27). Thus, growth rate of grouped offspring increased with age of parents, and was not maximized even in grouped nymphs unless the parents were more than one month old.

Johnston and McFarlane (1973) found no such increase in growth rate and their conclusion with regard to maternal influence was quite opposite from that of Chauvin. In their experiments, male nymphs from parents of all ages grew significantly faster than isolated ones, but females only did so if the parents were four weeks or less post adult emergence.

I did not make a special study of effect of parental age on responsiveness to grouping, but I kept records of the age of the parents of all nymphs used in experiments which I carried out. These data were tabulated for all experiments reported in this thesis which included grouped and isolated treatments and which were pursued to adult emergence of all nymphs.

2.8.2 Results

Table 7 shows sample sizes, means and standard deviations for grouped and isolated control treatments in eight experiments. Parental age ranged from 2-3 weeks to 6-7 weeks. There was no change in responsiveness to grouping related to increasing parental age. In two experiments males in isolation had growth rates insignificantly slower than those of grouped males, but the parents in one experiment were less than four weeks old and in the other, 5-6 weeks old.

I did not find that growth rate of offspring of older parents was any faster at the same temperature than that of the offspring of younger ones. Neither did female offspring of older mothers grow as fast in isolation as in groups. Females from parents of all ages grew significantly faster in groups.

I think the difference in results among Chauvin's (1958) , Johnston and McFarlane's (1973) and my experiments is probably related to sample sizes used in the experiments reported. Both Chauvin and Johnston and McFarlane used initial sample sizes of about 30 nymphs, which resulted in samples of 10-20 of either sex, depending on sex-ratio and mortality. Samples of this size are adequate for parametric analysis only if variability within them is relatively low.

Table 7

Comparison of mean developmental periods of grouped and isolated nymphs in eight experiments, related to age of parents (at 31.5°C).

	Males				Females				
Experiment	Isolated n	Isolated $\bar{x}\pm s$	Grouped n	Grouped $\bar{x}\pm s$	Isolated n	Isolated $\bar{x}\pm s$	Grouped n	Grouped $\bar{x}\pm s$	Age of parents (post emergence)
2	21	40.00±3.22	24	37.25±2.00**	20	39.80±3.36	24	36.25±2.49**	2 - 3 weeks
5	23	50.61±3.08	53	49.71±1.97^{ns}	22	49.91±3.48	37	47.63±1.53**	3 - 4 weeks
11	24	47.62±3.74	31	44.58±2.93**	23	47.04±4.25	31	42.04±3.42**	3 - 4 weeks
6	24	46.67±4.46	37	42.54±2.64**	28	44.78±3.19	25	40.56±2.71**	3 - 4 weeks
12	21	214.48±18.92	14	194.00±14.52**	17	197.65±23.93	13	176.92±15.08**	3 - 4 weeks
8	26	42.31±2.60	28	39.61±2.33**	31	41.45±4.38	24	38.33±2.18**	5 weeks
10	20	44.50±4.60	21	42.43±2.69^{ns}	17	45.53±6.44	23	39.13±2.45**	5 - 6 weeks
4	14	46.07±4.27	74	41.50±2.36**	11	47.18±4.53	100	40.65±2.43**	6 - 7 weeks

** = significantly faster developmental rate than isolated nymphs of same sex ($P<0.01$).

ns = insifnificantly faster developmental rate than isolated nymphs of same sex.

s = standard deviation.

So far, no maternal influence on response to grouping has been conclusively demonstrated. The great difference in growth rates between experiments in Chauvin's results suggests that the incubators which he used may have been liable to temperature fluctuations, since the phenomenon has not been demonstrated again, and growth rate appears to have been optimised by grouping without regard to parental age.

The fact that isolated males grew nearly as fast as grouped ones in two out of the seven experiments in Table 7, supports Johnston and McFarlane's (1973) observation that growth rate is more variable in that sex than in females.

2.8.3 Summary

1) There was no difference in growth rate of grouped nymphs of either sex in relation to age of parents.

2) The growth rate of isolated nymphs from parents 6-7 weeks old was slower than that of grouped nymphs, and there was no disappearance of sensitivity to grouping correlated with increasing parental age.

2.9 General Discussion and Conclusions of Section 2

Results of Experiments 1 and 2, together with measurements of temperature and humidity within rearing jars, show that faster growth in grouped crickets was not just the result of improving the physical environment of the nymphs. This implies that the phenomenon is one likely to be found in natural populations, not merely a result of experimental procedures. The presence of just one other nymph was sufficient to increase the growth rate to the optimum possible on the diet available.

Grouped crickets grew faster than isolated ones because they ate relatively more food per milligram of body weight and converted it to body tissue more efficiently. Since there was already a highly significant difference in weight of grouped and isolated nymphs by the end of the fourth instar, it seems reasonable that these differences in behavior and physiology were established early in nymphal life. The faster weight gain of grouped nymphs in any instar enabled them to pass through each instar more quickly, and to attain the weight which is associated with the development of wing-buds and the start of the last two nymphal instars more quickly.

The stimuli which induced faster food consumption and assimilation in nymphs of A. domesticus, could be provided by the presence of members of other species. Contact with a substrate recently used by members of the same species, however, produced only a small and insignificant increase in growth rate, and this was detected in female nymphs only.

These results suggest that feeding behavior is responsive to the physical presence of other nymphs rather than to a chemical laid down on the substrate, even though the attraction of used substrates for crickets of all ages is pronounced. If a chemical of any type is involved, it is probably not the stable arrestant which stimulates nymphs to rest on used resting sites. It is probably much more volatile, and associated with the recent or actual presence of other nymphs. However, the pheromone which promotes group cohesiveness is the primary means by which nymphs can be brought into contact with each other, and that contact maintained. This must be of the greatest importance in optimizing developmental rate.

Contact between nymphs in the arena studies always involved investigation of the other nymph by antennal contact. Nymphs did not appear to be aware of each other until such contact was made. The antennae of A. domesticus of all instars carry 3 types of chemoreceptors and 3 types of mechanoreceptors (Fudalewicz-Niemozyk and Rosciszewska, 1973), so that antennal contact may convey many types of information. For example, Ronse and Loher (1977) found that adult males of Teleogryllus commodus were able to detect the sex of another adult by antennal contact with the antenna of the other adult only.

Tactile stimuli were apparently responsible for faster growth in grouped nymphs of Blattella germanica (L.) (Ishii, 1971), increased macroptery in adults from grouped nymphs of Scapsipedus aspersus (Walker) (Saeki, 1966), and decreased pigmentation in grouped individuals of Gryllus bimaculatus (de Geer) (Levita, 1962).

In Ishii's experiments (1971), normal nymphs of B. germanica paired with chronically antennectomized nymphs grew more slowly than did nymphs in normal pairs (although not nearly as slowly as did the antennaless nymph). This result indicates that it may be important for a nymph to be touched by a companion's antennae, during development, as well as being able to touch its companion. Also, Ellis (1959) found that nymphs of L. migratoria migratorioides could be stimulated to develop gregarious behavior by the touch of wires trailing from a rotating ceiling.

The fact that nymphs of other species in another genus were able to stimulate growth to optimal rate in nymphs of A. domesticus increases the probability that the most important stimulation was tactile. It is possible that chemical cues of some kind may act in combination with physical ones in promoting optimum growth rate. Although my results do not suggest a major role for contact chemicals, olfactory stimulation as an agent was not eliminated by my experiments.

It is unlikely, however, that the olfactory cues provided by Gryllus nymphs would exactly resemble those of A. domesticus nymphs. The fact that experiments have been consistently carried out with all nymphs housed in the same incubator also reduces the likelihood of a volatile compound being responsible for the acceleration.

If faster growth rate requires the actual physical presence of another insect in order to occur, as my results suggest, then the nymphs' reaction to each others' presence by increasing the amount of food they eat comes into the category of social facilitation, as defined by Wilson (1975, page 51). Social facilitation does not imply any type of co-operation between nymphs. They need not forage together or eat at the same time. It merely indicates that the presence of another nymph increases occurrence of a certain behavior, in this instance, feeding. It may be that the presence of another nymph increases general activity, perhaps because of antennal stimulation, and that this restlessness leads to more contact with food, which results in feeding. Alternatively, increased restlessness might increase body temperature slightly and improve their efficiency in feeding and digestion. Such an increase in body temperature would probably not be detectable by measurement of environmental temperature.

I did not find any relationship between maternal age and growth rate, in the stocks which I used, but females apparently responded more consistently to environmental conditions than did males.

It is possible that a combination of stimuli, physical and chemical, is involved in facilitating feeding and optimizing growth rate. However, whether the stimuli are purely physical or partly physical and partly chemical, it does not seem as though the age of the parents has any effect on the susceptibility of nymphs to influences from their companions.

3.0 WHAT IS THE ADAPTIVE VALUE OF OPTIMIZING GROWTH RATE IN GROUPS?

3.1 Introduction to Section 3.0

The experiments reported in this section were designed to answer several questions on the nature of the response of nymphs to each other, including how it may be altered in different circumstances and whether it has any effects in adult life. The answers to these questions might suggest the adaptive value of faster growth in grouped nymphs in this species. Experiments with nymphs of other species show whether their biological strategies are similar to those of A. domesticus in this respect.

3.2 Materials and Methods

The same rearing procedures were used as were described in Section 2.2. In addition to the stocks of A. domesticus, G. fultoni and G. veletis from Indiana, mentioned in 2.2, stocks of G. veletis and G. pennsylvanicus from Alberta were used.

The Alberta stock of G. veletis was founded from three females and two males collected near Empress in southern Alberta, on May 24th, 1976. A stock of G. pennsylvanicus (Burmeister) was founded from about 50 late instar nymphs and adults collected at Warner, in southern Alberta, in late August, 1975.

Eggs of G. pennsylvanicus must be held at 5°C for 3 months or more to ensure their synchronous development, because there is a period of embryonic diapause which is broken by exposure to low temperatures. Afterwards, they all hatch in about 12 days at 31°C, like eggs of A. domesticus (Harris and Svec, 1964).

3.3 Is Growth Rate Responsive to Rearing Conditions Throughout Life?

3.3.1 Introduction to 3.3

Chauvin (1958) grouped nymphs of *A. domesticus* for the first 10 days of their lives, and then isolated them. He also isolated nymphs for the first 10 days, then grouped them. In both cases, the nymphs were as heavy at 30 days as were control nymphs which had been grouped throughout their lives. He concluded that the influence of grouping on developmental rate predominated over that of isolation, regardless of the stage at which it occurred. Nymphs of *B. germanica*, however, showed intermediate growth rates when grouped for only part of their developmental period (Izutsu et al., 1970). There was no domination of one experience over the other in effect on development, nor any critical stage at which growth rate was determined for the whole nymphal period.

I allowed all nymphs for each experiment to hatch in one container, so that nymphs in isolated treatments had had contact with others before the experiment began, for about one day in most instances. This did not prevent differences in growth rate between treatments from appearing, so that growth rate cannot be cued from stimuli received over a short period at the beginning of development. I wished to find out if changing conditions during later instars would modify growth rate.

3.3.2 Experiments 8 and 9

3.3.2.1 Procedure in Experiment 8: One hundred and sixty nymphs in pairs and the same number in isolation were reared at 31°C, and weighed at 22 days. They were in approximately the latter half of the sixth instar. At 25 days, half of the grouped nymphs were isolated, and the rest left in groups as a control treatment. Half of the isolated nymphs were grouped, and the rest continued to be isolated, as another control treatment. There was a highly significant difference in weight between paired and isolated treatments ($P<0.001$) (Table 8). When the reorganization was carried out, nymphs were allocated to treatments on the basis of weight, to make the two subsamples from each original treatment as comparable as possible (Table 9). The crickets were reweighed at 41 days, and their emergence to adults recorded.

3.3.2.2 Results of Experiment 8: Figure 10 shows cumulative emergence to adult. As expected from the results shown in Table 8, those in control pairs emerged significantly faster than those isolated throughout development. The mean developmental period of nymphs isolated at 25 days was slightly longer than that of control pairs, but the difference between these two treatments was not significant in either sex ($P<0.05$). Female nymphs paired at

Table 8

Experiment 8, mean weights in mg (± standard deviation) at 22 days.

Isolated	$59.07 \pm 21.91^{***}$
sample size	222
Grouped	77.34 ± 18.52
sample size	202

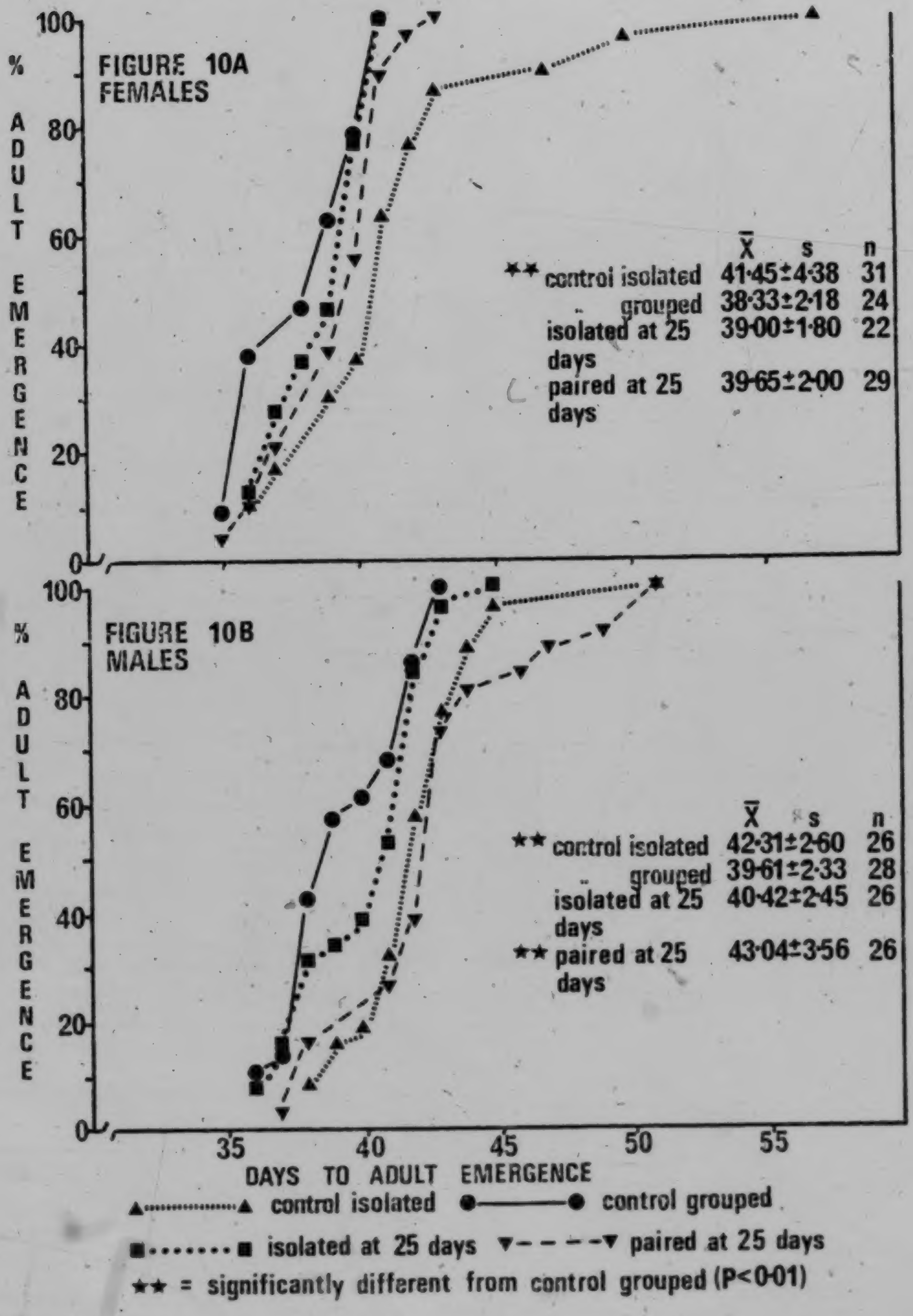
*** = significantly lighter than paired nymphs ($P<0.001$).

Table 9

Experiment 8, mean weights in mg (± standard deviation) at 22 days after hatching of nymphs assigned to new treatments.

	From isolated treatment		From paired treatment	
	Continued isolated	Paired at 25 days	Separated at 25 days	Continued paired
	57.09±23.00	61.35±21.07	76.65±18.24	77.65±18.80
sample size	54	56	50	51

Fig. 10. Cumulative adult emergence (days) in Experiment 8, on development of nymphs paired for part of development only.



25 days emerged faster than isolated females throughout life (fig. 10A). Their maturation rate was intermediate between those of the grouped and isolated control treatments. However, males paired at 25 days developed no faster than those isolated throughout life (fig. 10B) and in fact their mean emergence period is slightly longer.

By 41 days, when the crickets were weighed again, most of them had become adult. At this stage there were no significant weight differences among males in various treatments (Table 10). However, females, which begin to mature eggs after they emerge as adults, and consequently continue to gain weight, did show significant differences between treatments (Table 10). Females in control pairs tended to be heaviest ($\bar{x}$=519.67 mg), followed by females paired at 25 days ($\bar{x}$=478.14 mg). These latter females were heavier than females separated at 25 days ($\bar{x}$=457.82 mg) although they matured more slowly ($\bar{x}$=39.65 versus 39.00 days). This suggested that grouping was accelerating their post-emergence weight gain. Such effects were investigated further in another experiment and will be discussed in Section 3.7. Isolated females, which were not all adults when weighed, tended to weigh less ($\bar{x}$=433.13 mg) than those in other treatments, and differed significantly from paired females ($P<0.01$) and from those paired at 25 days ($P<0.05$). There is no evidence of significant reduction in growth in either sex.

Table 10

Experiment 8, mean weights in mg at 41 days (± standard deviation) and mean developmental period in days.

	Males		Females	
	Weight	Developmental period	Weight	Developmental period
Isolated	422.36 ± 55.26	$42.31^{**} \pm 2.60$	$433.13^{**} \pm 108.15$	$41.45^{**} \pm 4.38$
sample size	26	26	30	31
Paired at 25 days	438.63 ± 78.63	$43.04^{**} \pm 3.56$	$478.14^{\#} \pm 66.11$	$39.65^{\#} \pm 2.00$
sample size	26	26	29	29
Separated at 25 days	437.21 ± 54.02	$40.42^{\#} \pm 2.45$	$457.82^{*} \pm 56.48$	$39.00^{\#\#} \pm 1.80$
sample size	26	26	22	22
Paired	424.75 ± 51.39	$39.61^{\#\#} \pm 2.33$	519.67 ± 74.28	$38.33^{\#\#} \pm 2.18$
sample size	28	28	24	24

Significantly different from same sex of paired treatment: * ($P<0.05$); ** ($P<0.01$).

Significantly different from same sex of isolated treatment: # ($P<0.05$); ## ($P<0.01$).

Female nymphs grew significantly faster after being paired at 25 days (fig. 10A), but male nymphs did not (fig. 10B), which contrasts with Chauvin's (1958) findings, and with those of Izutsu et al. (1970). I did not expect that nymphs grouped at 25 days would emerge as rapidly as those paired throughout life, although Chauvin did not find any weight differences at 30 days between nymphs from different treatments, because to achieve comparable emergence would have required that nymphs grew faster after grouping than they usually did in groups. However, the difference between males and females is striking, and like the results of experiments on chemical stimulation (Section 2.5), it suggests that males and females differ in their capacity to respond to grouping. These results suggest that males lose this capacity during the latter part of nymphal growth, but that females do not.

3.3.2.3. Procedure in Experiment 9: Experiment 9 was carried out to determine if food consumption changed when nymphs were isolated from a group half-way through nymphal life. Nymphs as close to the end of the fifth instar as possible were selected, and there was no initial difference in weight between treatments. Nymphs were weighed at five day intervals for 15 days, and their food consumption over that period measured, as in Experiment 3. Faeces were not weighed but adult emergence was recorded.

As it became possible to distinguish sexes, it was found that there was a great preponderance of males in the samples, and that there were the same number of isolated males as grouped males in all male groups (22). For this reason, the comparisons were made between males only.

3.3.2.4. Results of Experiment 9, and Discussion of Both Experiments: Table 11 shows the results. No significant differences in weight developed between treatments over the course of the study. Weight gains and amounts of food consumed were similar. There were no significant differences in consumption index (CI), relative growth rate (GR) or efficiency of conversion of ingested food (ECI). The mean developmental period was exactly the same for both treatments.

Thus, isolation half-way through life did not in any way reduce growth rate. Results of Experiment 3 suggested that food consumption was influenced by social facilitation, but since CI remained the same after isolation, the phenomenon does not require the continued presence of another nymph throughout development and so resembles learning more than social facilitation. Alternatively, more efficient digestion in grouped nymphs could result in faster passage of food through the gut, leading to more frequent eating. Efficiency of digestion may be the result of the degree to which the digestive enzyme systems are induced, possibly controlled by hormone titres in the blood.

Table 11

Food consumption, weight gain and adult emergence of male *A. domesticus* nymphs in groups throughout life or separated at 30 days (28°C).

	Mean weight ± standard deviation (mg)									
	30 days	35 days	40 days	45 days	Wt. gain	Food eaten	CI	GR	ECI	Developmental period (days)
Grouped	47.30	100.99	144.08	192.83	145.82	219.06	0.094	0.062	66.60	59.36
n = 22	±4.46	±9.30	±19.24	±14.52	±9.78	±9.79	±.006	±.001	±2.16	±1.05
(8 groups)										
isolated	48.30	102.79	141.70	195.72	147.41	214.50	0.091	0.062	69.13	59.36
n = 22	±4.79	±7.86	±14.34	±19.00	±15.40	±28.22	±.008	±.001	±6.01	±1.09
t value	0.73	0.70	0.47	0.57	0.33	0.65	1.03	0	1.49	0

There are no significant differences between treatments ($P<0.05$).

In Experiment 8 there was a slight, though non-significant, tendency for nymphs to grow more slowly after isolation, though they were isolated for only one-third of their development. No sign of this was found in Experiment 9. It is possible that because nymphs isolated from a large group had had more constant feeding stimulation than had those in pairs, the feeding rate became more firmly established.

3.3.3 Summary

1) Nymphs of both sexes isolated from pairs had slightly longer mean developmental periods than those paired throughout life, but the degree of retardation was not significant, at $P<0.05$.

2) Only female nymphs grew faster after pairing at 25 days. Their growth rate was not significantly slower than that of females paired throughout development. Isolated males paired at 25 days matured no faster than males that remained isolated.

3) Male nymphs isolated from dense groups half-way through nymphal life continued to grow at the same rate as nymphs remaining grouped. Their consumption indices did not decline, and their developmental period was of the same mean length.

3.4 Does Group Composition Affect Growth Rate?

3.4.1 Introduction to 3.4

All previous authors who worked on "grouping effects" in crickets used groups of individuals of equal age. Wild populations, studied on English refuse dumps by Bate (1969a) were found to consist of crickets of all sizes during most of the year.

Izutsu, Ueda and Ishii (1970) worked on developmental rates of members of Blattella germanica. Nymphs of this species, like those of several other cockroaches (Guthrie and Tindall, 1968) grow significantly faster in groups than singly. Izutsu et al., (1970) carried out experiments in which a newly-hatched nymph was paired with another of the same age, or with a second instar nymph, a fourth instar nymph, or an adult. They concluded that growth rate of a nymph was faster in a pair regardless of the age of its partner, compared with the rate in isolation.

Norris (1962, 1964), working on Schistocerca gregaria (Acrididae), found that the presence of locusts of differing physiological age greatly affected each other's rate of development. While the presence of sexually mature males accelerated development of younger adult males, continuous association with very young nymphs retarded their maturation. In groups of Locusta migratoria, the presence of mature males accelerated development of nymphs. Norris attributed all these phenomena to the effect of pheromones produced by locusts at different ages.

I wished to determine if the growth rate of a nymph paired or grouped with larger or smaller individuals would be the same as when in contact with a peer.

3.4.2 Experiments 10 and 11

3.4.2.1 Procedure in Experiment 10: In Experiment 10, first instar nymphs were paired with 22 day old nymphs chosen from stock jars. The older nymphs were in approximately the 6th instar. The growth rates of both older and younger nymphs paired together were compared with those of similar nymphs reared in pairs or in isolation. There were initially 48 nymphs in each treatment, incubated throughout at 31.5°C. Older nymphs were weighed before the experiment began and at 37 days. Younger nymphs were weighed at 16 and 31 days, and at emergence to adult.

3.4.2.2. Results of Experiment 10: Table 12 shows weights of older nymphs at 22 days to be comparable between treatments. No significant differences developed during the course of the experiment and older nymphs emerged over approximately the same period whether isolated, in a peer pair or paired with a younger nymph (fig. 11). There were no significant differences in weight between treatments at 37 days (Table 13). The results for all treatments are similar to those of Experiment 9 and indicate that there was no decline

Table 12

Experiment 10, mean weights in mg (± standard deviation) of nymphs reared in a dense culture, at age 22 days when they were assigned to 3 different treatments.

	Paired with peer	Isolated	Paired with first-instar nymph
	76.84±13.19	77.01±11.84	77.28±13.43
sample size	48	48	48

There are no significant differences among these values ($P<0.05$).

Fig. 11. Cumulative adult emergence (days) of older nymphs in Experiment 10, comparing development of nymphs paired with a younger nymph at 23 days, with those of those isolated or placed in peer pairs at that time.

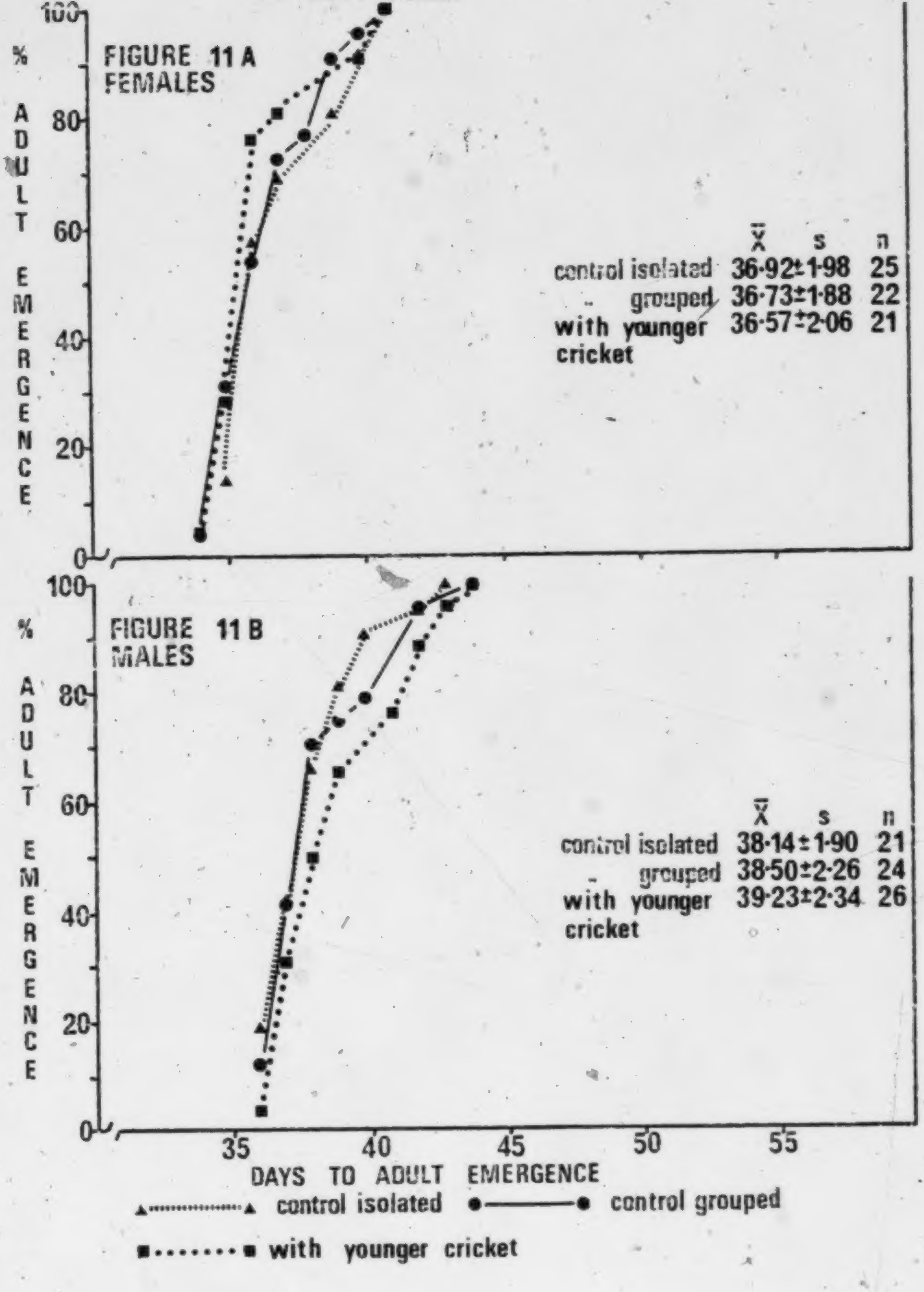


Table 13

Experiment 10, mean weights in mg (± standard deviation) of nymphs at 37-38 days (15-16 days after assignment to new treatments).

	Paired with peer	Isolated	Paired with younger nymph
Males			
	338.74±55.26	332.33±36.48	353.35±55.96
sample size	23	21	24
Females			
	434.14±71.79	410.33±56.77	415.77±39.59
sample size	23	26	20

There are no significant differences between treatment means for subjects of the same sex (P<0.05).

in consumption rate, or growth rate, following isolation from a group. Pairing with a younger nymph did not have any significant effect on growth rate in either sex although males matured slightly more slowly than in other treatments.

Table 14 shows weights of younger nymphs and Figure 12 shows their adult emergence. At 16 days, nymphs paired with older nymphs were not significantly lighter than nymphs paired with peers, while nymphs in isolation were so. Female nymphs paired with older nymphs were significantly heavier than those in isolation. Male nymphs paired with older nymphs were heavier than isolated males, which in this experiment grew faster than isolated females. By 30 days however, their growth rate had slowed considerably so that they were significantly lighter than those in control pairs. Figure 12 shows that they emerged as adults as slowly as, or more slowly then, nymphs in isolation and significantly more slowly than nymphs paired with peers. Isolated males in this experiment, although lagging behind peer pairs in weight gain, and in adult emergence, did not have a significantly longer developmental period than paired males.

However, although nymphs paired with older nymphs matured slowly, their weights at emergence were highly significantly heavier than those of subjects in other treatments (Table 14).

When samples were sub-divided depending on the sex

Table 14

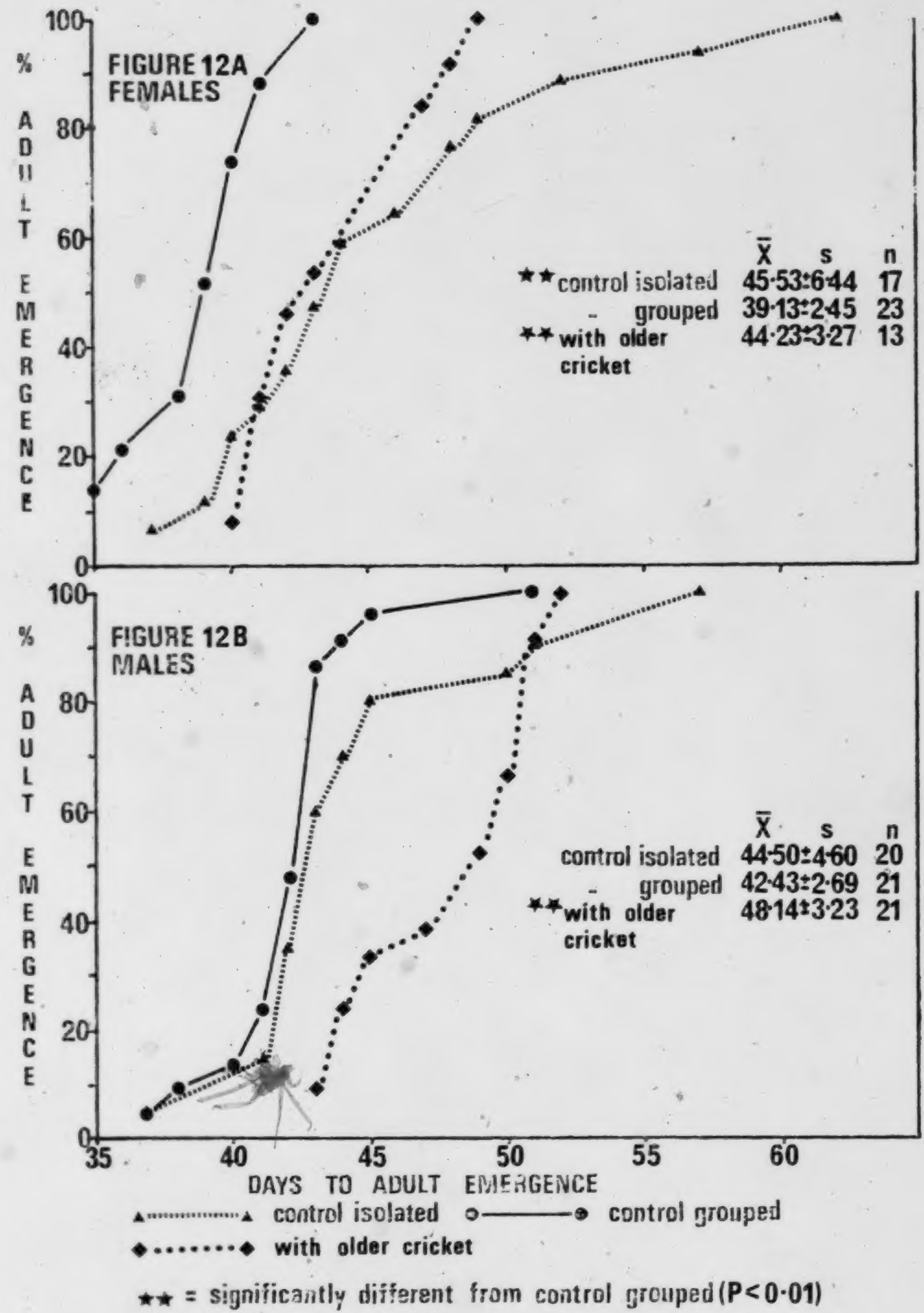
Experiment 10, mean weights in mg during development (± standard deviation).

	16 days	30 days	Adult emergence
Males			
with older cricket n = 21	21.79±4.98	177.10±54.27**	413.68±48.27$^{**\#\#}$
isolated n = 21	18.49±9.01*	192.86±77.89*	378.03±45.50
paired with peer	24.05±7.50 n = 13	235.57±58.80 n = 21	384.08±45.92 n = 21
Females			
with older cricket n = 13	21.68±2.87$^{\#\#}$	190.25±39.31**	437.19±60.70$^{**\#\#}$
isolated	14.46±7.41** n = 20	167.55±90.41** n = 19	386.62±54.40 n = 17
paired with peer	25.64±9.64$^{\#\#}$ n = 14	263.12±78.92$^{\#\#}$ n = 23	382.77±38.51 n = 22

Significantly different from subjects of same sex in paired treatment; * ($P<0.05$); ** ($P<0.01$).

Significantly different from subjects of same sex in isolated treatment; # ($P<0.05$); ## ($P<0.01$).

Fig. 12. Cumulative adult emergence (days) of younger nymphs in Experiment 10, on development of nymphs paired with older crickets.



of the older partner (Table 15), it was revealed that the nymphs which were heaviest were those which had been paired with an older individual of the same sex. In females the difference between sub-samples was not significantly great, and all females in this treatment tended to be heavier than those in other treatments. Males paired with older males were highly significantly heavier than males paired with females, which were no heavier than males in other treatments. No such differences occurred in either sex in nymphs paired with peers, for which the corresponding comparisons are also shown in Table 15. As Table 15 also shows, there was a slight tendency, not significantly great in samples of this size, for nymphs paired with one of their own sex to emerge as adults more slowly than those paired with a nymph of opposite sex.

The pattern of growth shown by nymphs grouped with older nymphs suggests that, until about the fifth or sixth instar, the presence of an older cricket affected food consumption and growth rate positively, even if not so strongly as did the presence of a peer. Later the effect ceased to be stimulatory and growth rate declined. This decrease seemed to coincide with the emergence of the older nymphs as adults.

Two possible explanations exist for this phenomenon. Either adult crickets no longer produce some type of stimulant, or their presence changes the behavior or metabol-

Table 15

Experiment 10, comparison of growth rate in relation to sex of older companion (mean weights ± standard deviation).

	Nymphs grouped with peers		Nymphs grouped with older crickets	
	Weight at emergence	Developmental period (days)	Weight at emergence	Developmental period (days)
Males with males	393.89±45.81 n = 12	42.75±2.96 n = 12	433.35±36.88** n = 15	48.40±2.97 n = 15
with females	371.01±4[illegible]28 n = 9	42.00±2.40 n = 9	355.00±23.86 n = 5	47.50±4.04 n = 6
Females with females	375.93±44.13 n = 14	39.21±2.83 n = 14	457.41±59.17 n = 7	45.00±3.26 n = 7
with males	394.74±23.96 n = 8	39.00±1.87 n = 9	420.60±63.41 n = 6	43.33±3.32 n = 6

** highly significantly heavier than males with females, P<0.01.

ism of the younger nymph.

It is notable that nine nymphs were lost between the first and second weighings in this treatment, in the period just after the older nymphs had emerged as adults. There was no corresponding mortality among either paired or isolated control nymphs, and after 30 days, no further mortality occurred in the mixed age treatment either. Because of this and because nymphs may be isolated during the latter half of their life-span without suffering any significant reduction in growth rate, the latter hypothesis seemed more likely to be true.

In order to test the hypothesis, Experiment 11 was carried out.

3.4.2.3 Procedure in Experiment 11: In this experiment, two first instar nymphs were grouped with one older one, with grouped and isolated first instar nymphs as controls. If the presence of a peer negated the effect of having an older companion and restored normal growth-rate, it would indicate that growth rate of single nymphs declined due to lack of stimulation. If the growth rates of both nymphs were slower, it would indicate that the growth rate was retarded because of harassment by the older cricket.

There were initially 60 nymphs in each treatment, except older nymphs used in groups with two younger ones, of which there were only 30. Older nymphs had been reared in groups of four for 23 days and were in the fifth or sixth instar. They were allocated to treatment randomly, and were not weighed before the experiment started, but were weighed at 36 days. Younger nymphs were not weighed although I had intended to do so, because I was ill at the time.

3.4.2.4. Results of Experiment 11 and Discussion of Experiments 10 and 11: As in Experiment 10, no significant weight differences developed between older nymphs in different treatments up to 36 days, and adult emergence occurred over the same period in all three experiments.

Figure 13 shows adult emergence of younger nymphs. Development of nymphs grouped with older nymphs was intermediate in rate between nymphs grouped with peers only and those kept in isolation. In females, growth rate did not differ significantly from that of nymphs grouped with only peers, although the retardation is clear. In males, however, growth rate was significantly slower ($P<0.05$) compared with males grouped with peers, and not significantly faster than that of isolated males.

Table 16 shows these results subdivided according to the sex of the older nymph. The same trends appear as in the previous experiment (Table 15), and here too, there are no significant differences in emergence rate.

Thus it appears that growth rate of nymphs paired with older nymphs in Experiment 11 was retarded because of

Fig. 13. Cumulative adult emergence (days) of younger nymphs in Experiment 11, on development of nymphs paired with both an older cricket and a peer.

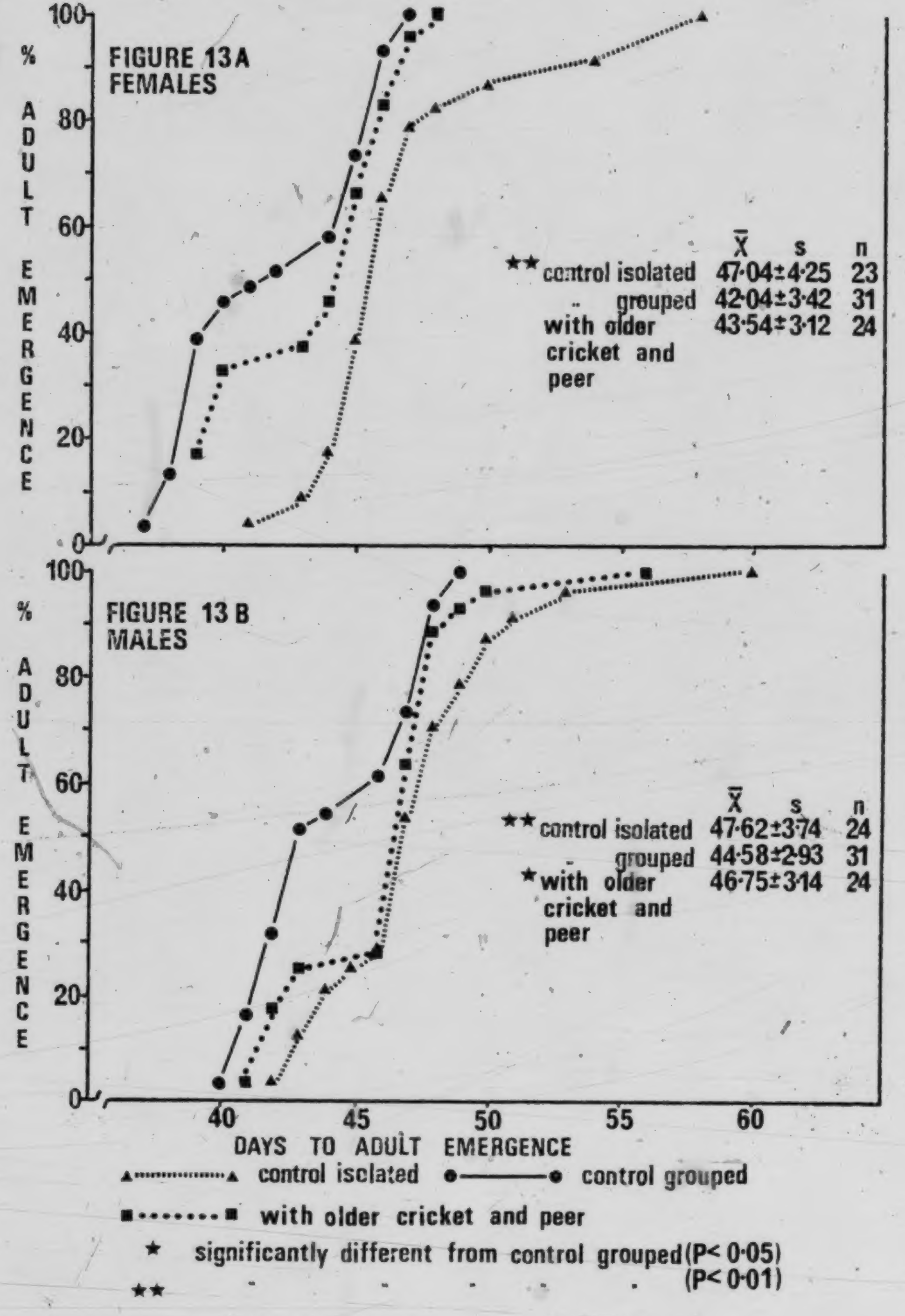


Table 16

Experiment 11, developmental rates in days of younger nymphs related to sex of older cricket (± standard deviation)

	With same sex	With opposite sex
Males		
	47.00±1.84	44.36±3.85
sample size	11	14
Females		
	44.62±2.44	43.54±3.36
sample size	8	13

There are no significant differences among these values, except between males and females.

the presence of the older nymph rather than because of a lack of stimulation. The older nymph may have harassed the younger one during feeding, sending it into a crevice for protection, and so restricted its intake of food. Or it's presence alone may have stressed the younger nymph and caused it to eat less frequently. When two nymphs were present, they appeared to have stimulated each other's growth to a certain degree, more pronounced in females than males, but they did not eliminate the effect of having the older nymph present. Their mutual contact may have had a stress reducing effect. Certainly, they did not disappear during development like nymphs in this treatment in Experiment 10.

In Experiment 10, retardation of growth occurred only in later instars. My observations during the course of Experiment 11 were that nymphs with older nymphs grew as fast as those with peers in early instars, but later began to lag, so that they did not develop wing-buds as early as grouped controls. It seems plausible that newly emerged adults, beginning sexual maturation, became aggressive toward their younger companions.

In the table of results that Izutsu et al., (1970) presented, growth rates of first-instar nymphs of B. germanica paired with second instar nymphs or with adults of either sex were very similar to those of nymphs paired with others of the same age. However, growth rate of those paired with fourth instar nymphs was nearly as slow as that of those reared in isolation. They did not mention this discrepancy in their discussion. Either the figure is a misprint, or their results in that experiment resemble my own. B. germanica nymphs pass through six instars, so that the difference in developmental stage between first instar nymphs and fourth instar nymphs in that species is comparable to that between older and younger nymphs in my experiments.

The higher weight at maturation of nymphs reared with older crickets is very striking (Table 14). It is in keeping with the fact that these nymphs gained weight faster than isolated ones before a period of growth inhibition began. As the results of Experiment 3 showed, nymphs which did not gain quite enough weight to develop wing-buds at one moult, were well over the limiting weight by the next. It seems probable that growth rate declined most sharply one or two instars immediately preceding the earliest instar in which wing-pads could have become visible. If nymphs had maintained their earlier growth rate, they would have matured in one fewer instars, and their weights would have been like those of crickets in other treatments.

In both sexes, but more noticeably in males, nymphs in pairs with older nymphs of the opposite sex were less heavy at adult emergence than were nymphs with the same sex companion. They also tended to mature slightly earlier but not significantly so (Table 16). Table 17 shows that although males in this sub-group averaged 23.48±5.33 mg at 16 days, slightly heavier than males with males (21.11±4.85 mg), they were lighter at 31 days (166.25± 61.91 mg, in contrast with 181.44±52.62 mg. for males with males). This suggests that, in that sub-group, retardation may have begun earlier. However, sample sizes in all sub-groups are too small to encourage anything but tentative hypotheses.

3.4.3 Summary

1) Nymphs paired with older nymphs grew as fast as nymphs paired with peers in early instars, but their growth rate declined in later instars. They emerged as slowly as, or more slowly than, isolated nymphs.

2) Nymphs grouped with a peer nymph and an older nymph developed at a rate intermediate between those grouped with peers and those in isolation. Females grew nearly as fast as those with peers, but males insignificantly faster than isolated males.

3) Nymphs paired with an older nymph were significantly heavier at adult emergence than were nymphs in either of the control treatments. In females this difference occurred both

Table 17

Experiment 11, mean weights during development and number of days to emergence of nymphs with older crickets (± standard deviation). Effect of sex of older cricket.

	Weight at 16 days (mg)	Weight at 31 days (mg)	Weight at emergence	Developmental period (days)
Males with males	21.11 ± 4.85	$181.44 \pm 52.62^{*}$	$433.25 \pm 30.88^{\#\#**}$	$48.40 \pm 2.97^{\#\#**}$
sample size	15	15	15	15
Males with females	23.48 ± 5.33	$166.25 \pm 61.91^{*}$	355.00 ± 23.86	$47.50 \pm 4.04^{*}$
sample size	6	6	5	6
Females with females	21.61 ± 3.72	$189.47 \pm 42.67^{*}$	$451.41 \pm 59.17^{**}$	$45.00 \pm 3.26^{**\#\#}$
sample size	7	7	7	7
Females with males	$21.77 \pm 1.77^{\#}$	$191.47 \pm 38.85^{*}$	420.60 ± 63.41	$43.33 \pm 3.32^{*}$
sample size	6	6	6	6

Significantly different from subjects of same sex in paired control treatment

* ($P<0.05$); ** ($P<0.01$).

Significantly different from subjects of same sex in isolated control treatment

# ($P<0.05$); \#\# ($P<0.01$).

in females paired with females and females paired with males. In males, it occurred only in males paired with males.

4) Older nymphs showed no significant differences in growth rate during the experiment, whether left in groups, isolated, or paired with a younger nymph. Younger nymphs appear to have no significant effect on growth rate of older ones.

3.5 Is Growth Rate Relatively Faster in Groups Reared at Lower Temperatures?

3.5.1 Introduction to 3.5

McFarlane (1966b) reported that at 29°C the mean development time of female nymphs of *A. domesticus* reared in groups was 74% that of isolated females, and that of grouped males, 79% that of isolated ones. The corresponding percentages at 35°C were 92% and 89%. He concluded that nymphs were more affected by grouping at the lower temperature and suggested that "the results indicate the while the group effect may be an academic consideration at 35°C, it is of real importance to the species at lower temperatures".

Fuzeau-Braesch and Ros's results (1965) suggested the same conclusion since grouped nymphs of *G. bimaculatus* grew significantly more quickly than isolated ones at lower temperatures than at higher ones, while at 36°C, isolated nymphs grew faster than grouped ones.

These results suggested that a lower temperature than the 29°C used by McFarlane would be associated with an even faster rate of development in grouped nymphs in comparison with that of isolated ones, so I tested the hypothesis with an experiment carried out at room temperature (20-23°C).

3.5.2 Procedure in Experiment 12

Experiment 12 comprised two treatments only, paired and isolated nymphs, which were reared at room temperature in an incubator which was not running. The room fluctuated between 20 and 23°C. There were originally 66 nymphs in each treatment, and they were weighed once during development, at 155 days.

3.5.3 Results

Mortality was much higher than in comparable experiments done at 31°C, 42.6% in both treatments, with 38 individuals surviving to maturity in each. However, death of 1 member of a pair eliminated the survivor from the treatment total, since inspections were not frequent enough to make re-pairing valid, and mortality was not synchronized anyway. Six females and five males were not included in the paired treatment total.

Paired nymphs were significantly heavier than isolated ones at 155 days as expected (Table 18), the mean of isolated nymph weights being about 65% that of grouped ones in both sexes. At the time of weighing only six paired nymphs were without wing-pads compared with 25 isolated ones.

The same significant differences between treatments occurred in emergence rates (fig. 14). The means differed by about 20 days for both sexes. Emergence was extended over 50 days for paired females and 80 days for isolated

Table 18

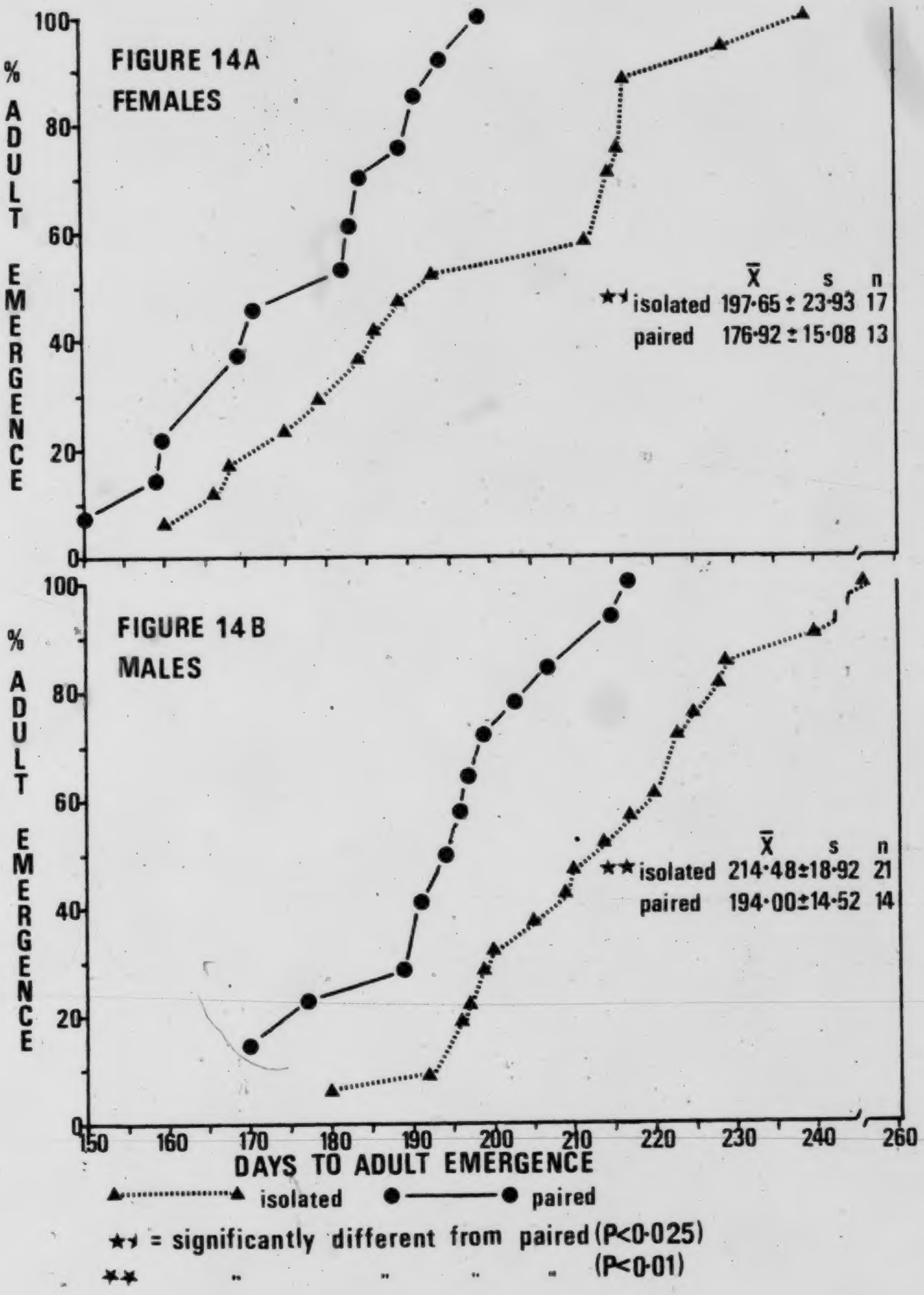
Experiment 12, mean weights in mg at age 155 days (± standard deviation).

	Isolated	Grouped
Males		
	134.21±54.75**	203.44±57.55
sample size	21	17
Females		
	153.02±101.82***	234.51±87.59
sample size	18	14

** = significantly different from subjects of same sex in groups ($P<0.025$).

***= significantly different from subjects of same sex in groups ($P<0.001$).

Fig. 14. Cumulative adult emergence (days) in Experiment 12, on developmental rates of paired and isolated individuals at 20-22°C.



ones. The corresponding ranges for males were 47 and 77 days.

Ghouri and McFarlane (1958) gave the mean duration of nymphal life at 23°C as 104 days for grouped males (n=12) and 114 days for females (n=13). The corresponding values in my experiment were 194.0 days (n=14) and 176.9 days (n=13), which suggests that mean room temperature was lower than 23°C, since my stock was from the same source as theirs. In this experiment also, females emerged faster than males in both treatments.

The mean developmental period in groups was 90.4% that of isolated individuals in males, and 89.5% in females.

3.5.4 Comparison with Other Experiments Reported In This Study, and Discussion

Table 19 shows the comparisons of means of developmental periods for grouped and isolated treatments from 8 experiments, carried out at a range of temperatures, arranged in order of increasing mean number of days to maturation in the grouped nymphs. Experiment 12 is included last in the series. Grouped female means were 85.9 to 95.4% those of isolated females, and those of grouped males, 90.0 to 98.2% those of isolated males. There is no clear relationship between speed of growth and relative growth rates in the two treatments, in either sex. The proportion of time in which grouped nymphs developed compared with isolat-

Table 19

Comparison of mean developmental periods in days of grouped and isolated nymphs in 8 experiments ($\pm$ standard deviation).

	Males					Females				
Experiment	n	Isolated $\bar{x} \pm s$	n	Grouped $\bar{x} \pm s$	Grouped mean as % of isolated mean	n	Isolated $\bar{x} \pm s$	n	Grouped $\bar{x} \pm s$	Grouped mean as % of isolated mean
2	21	40.00±3.22	24	37.25±2.00	93.1	20	39.80±3.36	24	36.25±2.49	91.1
8	26	42.31±2.60	28	39.61±2.33	93.6	31	41.45±4.38	24	38.33±2.18	92.5
10	20	44.50±4.60	21	42.43±2.69	95.3	17	45.53±6.44	23	39.13±2.45	85.9
4	14	46.07±4.27	74	41.50±2.36	90.0	11	47.18±4.53	100	40.65±2.43	86.1
6	24	46.67±4.46	37	42.54±2.64	91.1	28	44.78±3.19	25	40.56±2.71	90.6
11	24	47.62±3.74	31	44.58±2.93	93.6	23	47.04±4.25	31	42.04±3.42	89.4
5	23	50.61±3.08	53	49.71±1.97	98.2	22	49.91±3.48	37	47.62±1.53	95.4
12	21	214.48±18.92	14	194.00±14.52	90.4	17	197.65±23.93	13	176.92±15.08	89.5
average					93.2					90.1

ed nymphs was never as low in my experiments as they were in McFarlane's experiment at 29°C.

However, although there was no relative increase in growth rate in grouped nymphs at this lower temperature, the actual difference in mean developmental period was nearly three weeks and would presumably be even greater at still lower temperatures. Thus, grouped nymphs would become adults several weeks earlier than isolated ones in natural conditions even without any relative increase in speed of development. It is also notable that total emergence period for the grouped sample was shorter than that of the isolated sample, so that grouping tended to synchronize development.

3.5.5 Summary

1) The growth rate of grouped nymphs had the same relationship to that of isolated nymphs at 20-23°C as at 31.5°C. At all temperatures used, the mean developmental period of grouped males was between 90.0 and 98.2% that of isolated males, and of females, 85.9 to 95.4% that of isolated females.

3.6 Does Response to Grouping Differ Between Male and Female Nymphs?

3.6.1 Introduction to 3.6

In Section 2.8 I noted that the growth rate of males was more variable than that of females. In this section the mean developmental periods of males and females in grouped and isolated treatments from the same experiments (Table 7) are compared. The mean developmental period of females is expressed as a proportion of the mean developmental period of males for both treatments. These proportions were compared between treatments by non-parametric methods.

3.6.2 Results

Table 20 shows the results. Females in groups grew consistently faster than males in groups. Females in isolation did not. The mean developmental period of grouped females was a consistently smaller proportion of the mean developmental period of males in all experiments. The difference between treatments is significant ($P<0.01$, Wilcoxon's signed rank test).

This indicates that contact with other nymphs is a more important stimulus to growth in females than males. This is consistent with the results of Experiments 8 and 11.

Table 20

Developmental period of females expressed as a proportion of the developmental period of males, in 8 experiments from this study, in grouped and isolated treatments.

Experiment	Isolated	Grouped
2	.995	.973
8	.980	.968
10	1.023	.922
4	1.024	.979
6	.959	.953
11	.988	.946
5	.986	.958
12	.922	.912

Treatments differ significantly $P<0.01$ (Wilcoxon's signed rank test).

3.6.3 Summary

1) Female nymphs in peer groups had a shorter mean maturation time than males, in all experiments. Isolated females had a longer mean maturation time than males in two experiments.

2) The difference in growth rate between males and females was significantly smaller in isolated nymphs than in grouped ones.

3.7 Does Grouping or Isolation During Growth Affect Reproduction of Adult Females?

3.7.1 Introduction to 3.7

Speed of oogenesis and fecundity has been found to be related to population density in females of several species of Acrididae. The best-studied of these are locusts, especially Schistocerca gregaria (Forskal) and Locusta migratoria migratorioides (Reiche and Fairm). Isolated adult females of S. gregaria took longer to begin laying eggs than did those in crowds, while the situation was reversed in females of L. migratoria (Norris, 1950 , 1952, 1954). Mating, the presence of adult males, and daily periods of flying also accelerated development of eggs in females of S. gregaria (Norris, 1957) and flight accelerated development in crowded females of L. migratoria (Highnam and Haskell, 1964). Females of both species laid fewer eggs when kept in crowded conditions than when isolated.

Other species in which females laid fewer eggs when crowded include Melanoplus sanguinipes (Walker) (Smith, 1970), Eyprepocnemis plorans ornatipes (Walker) (Antoniou and Hunter-Jones, 1968) and Ornithacris turbida (Walker) (Antoniou, 1973). Crowded females of the two latter species tended to begin egg-laying earlier than did isolated ones. Crowded females of Schistocerca pallens (Antoniou and

Robinson, 1974) laid more eggs, and their fertility was also significantly higher than that of isolated females.

Bradley (1977), found that paired adult virgin females of A. domesticus developed more eggs by 11 days after adult emergence than did isolated ones, and that they had higher ovarian dry weights, and longer terminal and penultimate oocytes. He separated females from stock cultures of crickets in their penultimate instar. These data suggested that the first cycle of vitellogenesis occurred more rapidly in grouped females. However, the opposite result was found in females in larger groups, and pairs of females with a male matured fewer eggs in the first 10 days of adult life than did isolated virgins.

My experiment aimed to determine if grouping or isolation during development had any effect on how soon females of A. domesticus began to lay eggs, and on how many eggs they subsequently produced.

3.7.2 Procedure

I used 21 adult females from the paired control treatment of Experiment 11, and 25 from the isolated control treatment. They were removed from their original jars on the second day following adult emergence, and placed singly in clean jars with food, water, a sexually mature male and a one oz (∝ 30 ml) plastic cream cup full of moist sand for egg laying. A wire mesh disc over the sand helped the female to insert her ovipositor and prevented the parents from eating the eggs. The crickets continued to be incubated at 29°C.

Cups were inspected once daily for signs of oviposition, since the age of females was known only to within 24 hours. The sand in the cups was kept moist. The first day on which oviposition occurred was recorded, and the cup left with the female until the end of the fifth day after oviposition began, at which time the female was killed and frozen. After the fifth day, the eggs continued to be incubated, at 29°C. The number of first instar nymphs which hatched was recorded. Females were later dissected and chorionated eggs in their ovaries counted.

3.7.3 Results and Discussion

Table 21 shows that females reared in groups started laying eggs earlier than did previously isolated females. The difference was significant at $P<0.05$. The actual mean difference (0.79 of a day), was about 15% of the total grouped mean preoviposition period.

Two females did not produce any eggs for 7 days and I placed a second male in their jars. They both produced eggs during the following day. I assumed from this that the first males were unable to mate, since unmated females usually retain their eggs even when they are fully developed. These females were not included in the analysis.

Table 21

Preoviposition period in relation to treatment during development. Mean number of days between adult emergence and oviposition (± standard deviation).

	Isolated during development	Grouped during development
	5.59±1.39*	4.80±0.83
sample size	27	20

* = significantly longer than mean for subjects in groups ($P < 0.05$).

Since the females could not be included in the sample, I discontinued providing second males for later emerging females and some of these produced eggs after a 7 day preovipositional period or even longer, suggesting that the results for the two earlier females may have represented their true rate of development. One such female came from each experimental treatment.

Three females were overlooked for one day and were not killed until the sixth day after oviposition began, and they also were not included in the samples when analysis was done on numbers of progeny.

These results support Bradley's (1976) findings from experiments with paired and isolated virgin females, that vitellogenesis proceeded faster in grouped females. He found this result after separating nymphs from crowded stock jars only in the last nymphal instar, which may be the reason that differences between his treatments were not significant. In my study females were under different experimental conditions throughout their nymphal lives, and all under the same conditions as adults.

The preovipositional period of A. domesticus females has been reported as 21 days at 30.5°C (Schmidt and O'Brian, 1966), 12.8±9.5 days at 35°C, 36.2± 13.2 days at 26.5°C (Bate, 1971) and 8 to 39 days depending on temperature and season (Ahmad and Ghauri, 1953). These periods are all much longer than in either treatment in my study, but

Thomas (1964) recorded a preovipositional period of 8 days at 26°C. Preovipositional period is presumably influenced by diet and probably by population characteristics.

Over 5 days, females from groups produced a lower mean number of viable eggs than did those reared in isolation (Table 22) but the difference was not significant. Since they did not have a higher mean number of chorionated eggs in their ovarioles (Table 22), the difference in number of eggs already laid was not balanced by the number which would have been laid in the following few days. The 2 ovaries of one female were often of different size and contained different numbers of chorionated eggs. This finding agrees with that of Thomas (1964) who reported that females had 128 to 194 ovarioles in his study, with a mean of 154 ± 1.9 and that there was sometimes a difference of up to 20 ovarioles between ovaries in one female.

3.7.4 Anomalous Result Found in Some Members of [illegible]ated Treatment

Th[illegible] of the last isolated females to mature were found, when dissected, to have large pink thoracic wing muscles, that seemed capable of sustaining flight. All other females had small, white, degenerate muscles. According to Srihari, Gutmann and Novak (1975) the flight muscles of *A. domesticus* females usually reach their maximum development (at 28°C) about two days after adult eclosion and begin to de-

Table 22

Mean number of nymphs hatching from eggs laid over a 5 day period, and number of chorionated eggs remaining in ovarioles after 5 days (± standard deviation), in relation to treatment during development. All females in isolated treatment included.

	Isolated during development	Grouped during development
Number of nymphs		
	146.24±61.84	117.22±71.60
sample size	25	18
Number of chorionated eggs		
	86.95±71.03	85.88±50.51
sample size	21	17
Number of nymphs & number of chorionated eggs		
	237.19±89.22	205.76±75.98
sample size	21	17

There are no significant differences between treatment means ($P<0.05$).

generate soon afterwards. At lower temperatures (20-22°C) the period of usefulness for flight is 10-15 days (Chudakova and Bocharova-Messner, 1965). Thus, for females to have large pink muscles at 29°C after 10 or more days of adult life is remarkable. These females had laid a less than average number of fertile eggs, and had fewer chorionated eggs in their ovaries, so that excluding them from the sample made the difference between treatments larger (though still not significant) (Table 23, compare with Table 22). Bate (1969b) found that all females (except one) caught flying away from a natural population in a rubbish tip had mated, but that only one had any vitellogenic eggs in the ovaries. Evidence from implantation experiments by Belyaeva (1967) and Bradley (1976) and from extirpation experiments by Chaduakova and Bocharova-Messner (1968) indicated that as titres of juvenile hormone rose, yolk protein production increased and wing muscles were simultaneously broken down. Thus, the existence of large, functional-appearing flight muscles in females which had begun to lay is anomalous in comparison with the findings of other workers, which suggest that the 2 states are hormonally incompatible. These anomalous results cannot be explained at present, and their elucidation must await further work.

3.7.5 Summary

1) Females from groups began laying eggs significantly

Table 23

Mean number of nymphs hatching from eggs laid over a 5 day period and number of chorionated eggs remaining in ovarioles after 5 days (± standard deviation), in relation to treatment during development. Females with large pink wing muscles excluded from isolated treatment.

	Isolated during development	Grouped during development
Number of nymphs		
	160.83±61.98	117.22±71.60
sample size	18	18
Number of chorionated eggs		
	110.00±98.00	85.88±50.51
sample size	18	17
Number of nymphs & number of chorionated eggs		
	251.39±87.13	205.76±75.98
sample size	18	17

There are no significant differences between treatment means ($P<0.05$).

earlier than previously-isolated females. They tended to produce fewer fertile eggs during a 5-day period, and they also tended to have fewer eggs remaining in their ovarioles, but these differences were not significant.

2) Three late-maturing isolated females had functional flight muscles 5 days after they began laying eggs. These muscles had regressed in all other crickets. The latter result is consistent with those of earlier authors, but the former is anomalous.

3.8 Do Nymphs of Gryllus Species Respond to Grouping?

3.8.1 Introduction to 3.8

The primary reason for obtaining stocks of the North American field crickets *Gryllus veletis*, *G. fultoni* and *G. pennsylvanicus* was to carry out the experiments described in Section 2.7. Since stocks of each proved easy to maintain at least for several generations under laboratory conditions, it seemed an obvious course of action to determine whether these field crickets themselves displayed any reaction to grouping.

Populations of *G. veletis* and *G. fultoni* are usually quite small and widely scattered, and these crickets are not reported to be gregarious. Populations of *G. pennsylvanicus* can be large, and late instar nymphs and adults are often found in swarms. Adult males of this species are much less aggressive than those of *G. veletis*. Since high population density may be assumed to be normal for *G. pennsylvanicus* developmental rate might be optimized in such conditions. For this reason I considered it more likely that nymphs of *G. pennsylvanicus* would grow faster when reared in groups than those of *G. veletis*.

All three species which I used have one generation a year in their usual environments. The overwintering stages of *G. veletis* and *G. fultoni* are nymphs in the last 3 instars, the prolonged duration of which has already been mentioned in

Section 2 . Members of G. pennsylvanicus overwinter as eggs. **Some individuals** of all three species will develop without diapausing, as do members of A. domesticus, but for the majority, the delay is apparently obligatory. Since the developmental rates of members of all three species are so strongly related to seasonal change it seemed unlikely that accelerated development related to the presence of peers would have any adaptive value for them. I was interested in finding out from my experiments whether a faster growth rate would appear in grouped nymphs of these species, since this would indicate whether this phenomenon is a universal feature of cricket biology or a specific strategy of members of A. domesticus.

3.8.2 Procedure in Experiments 13, 14, 15 and 16

Experiments were carried out with four stocks, all founded from wild-caught females. These included the G. fultoni stock mentioned in Section 2.2.3, G. pennsylvanicus from Alberta, and two stocks of G. veletis, one from Indiana, and the other from Alberta. All four experiments had three treatments, isolated nymphs, groups of three and groups of six, so that effects of density as well as grouping could be assessed. Initial sample sizes were around 60 nymphs in all treatments and all experiments were incubated at 31°C. No light cycles were used except for about five days early in Experiment 14 with G. pennsylvanicus.

Humidity was raised in the jars during the first instar, as described in Section 2.2, except in the experiment with G. fultoni nymphs, which was carried out first, before the need to protect first-instar nymphs from desiccation was realized. Only nymphs of G. veletis from Alberta (in Experiment 16) were weighed during development, at 48 days.

3.8.3 Results and Discussion

3.8.3.1 Growth Rate: Experiment 13 with G. fultoni suffered very high mortality from desiccation of first instar nymphs, and final totals of adults were so low that both grouped treatments were combined for analysis. Table 24 shows that there were no significant differences in developmental period either between sexes or between treatments, so that this experiment detected no response to grouping in nymphs of G. fultoni. It was not repeated due to lack of a suitably large number of first instar nymphs.

Figure 15 shows cumulative emergence of adults of G. pennsylvanicus (Experiment 14). It can be seen that emergence was highly synchronized and that mean developmental period was shorter than would be found in nymphs of A. domesticus reared at the same temperature. Males took, on average, one day longer to emerge than females, but the cumulative emergence curves were similar for both sexes.

There was no significant acceleration of development

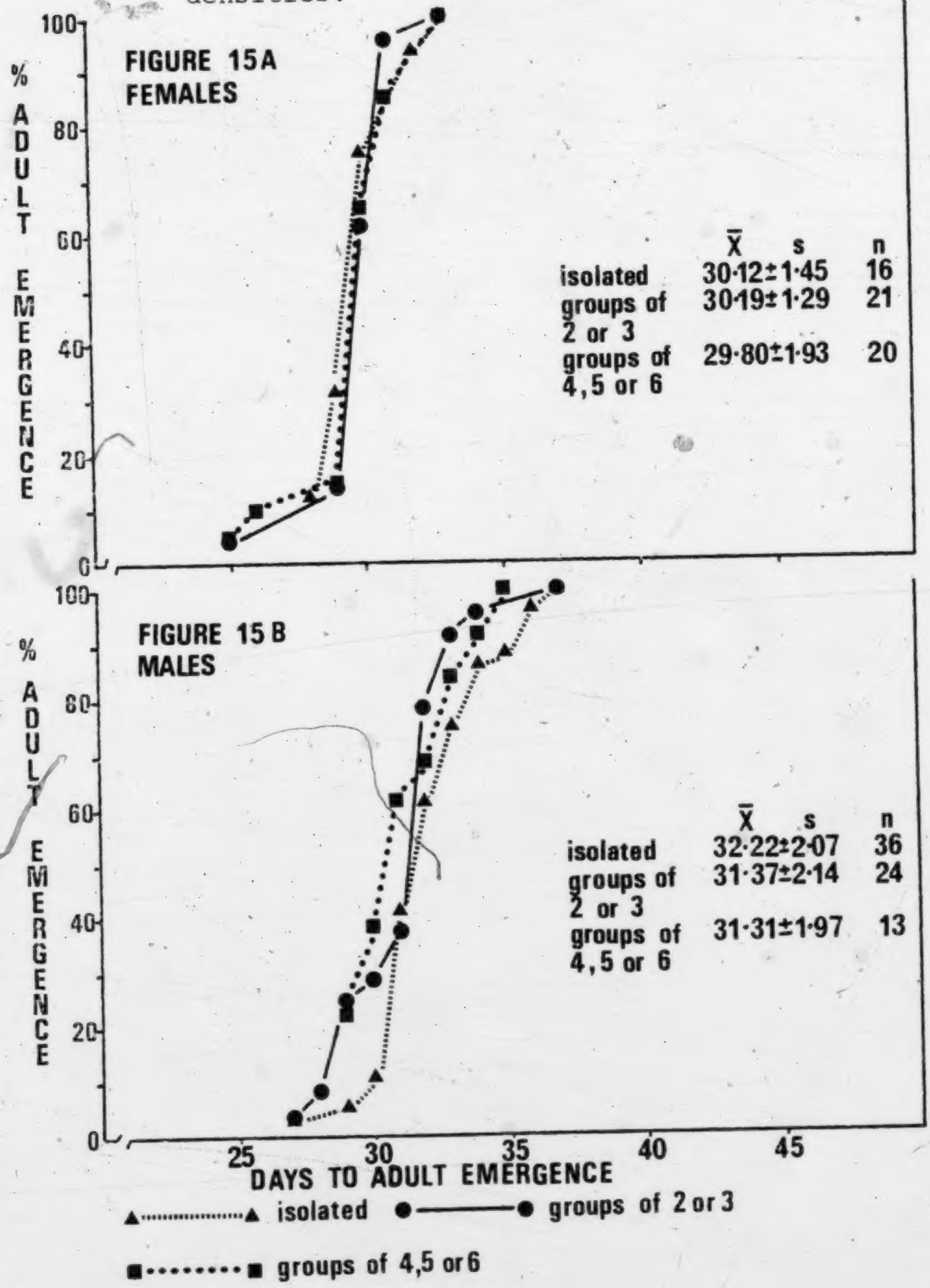
Table 24

Experiment 13, mean developmental period in days in nymphs of *G. fultoni* (± standard deviation).

	Grouped	Isolated
Males	79.6	91.0
	±15.75	± 6.44
	n=10	n=8
Females	82.12	83.0
	±11.83	±12.50
	n=17	n=10
Total	81.19	86.55
	±13.17	±10.79
	n=27	n=18

There are no significant differences among these values ($P<0.05$).

Fig. 15. Cumulative adult emergence (days) in Experiment 14, on developmental rates of individuals of Gryllus pennsylvanicus, in isolation and in groups of various densities.



related to grouping, although grouped females did begin emerging 3 days before isolated ones. The male to female ratio was 1.26:1.00 in the total experiment, but varied widely among treatments, being 2.25:1.00 for isolated nymphs, 1.14:1.00 for groups of 3 and 0.60:1.00 for groups of 6. The difference correlated with numbers of survivors in each treatment at adult emergence, 52 isolated, 45 in groups of 3 and 32 in larger groups. This suggests that members of groups were likely to be eaten by their peers, and that the more slowly developing males were more likely to be victims.

Figure 16 shows adult maturation patterns of G. veletis from southern Indiana (Experiment 15). Neither sex showed any significant acceleration when grouped. Mean developmental period was more than twice that of G. pennsylvanicus nymphs, which accords with the findings of Alexander and Bieglow (1960). Males and females showed similar mean developmental times, but, as in Experiment 14, there was probably a tendency for males to be killed before maturing. The male to female ratio was 0.82:1.00 among isolated nymphs (in which no predation could occur), 0.72:1.00 in groups of 3 and 0.52:1.00 in larger groups.

In G. veletis from southern Alberta (Experiment 16) there was no significant difference between treatments in weight at 48 days (Table 25). When male and female weights of isolated nymphs were compared, males averaged significantly lighter ($P<0.05$). Between 48 days and adult emergence there

Fig. 16. Cumulative adult emergence (days) in Experiment 15, on development of individuals of Gryllus veletis from southern Indiana, in isolation and in groups of various densities.

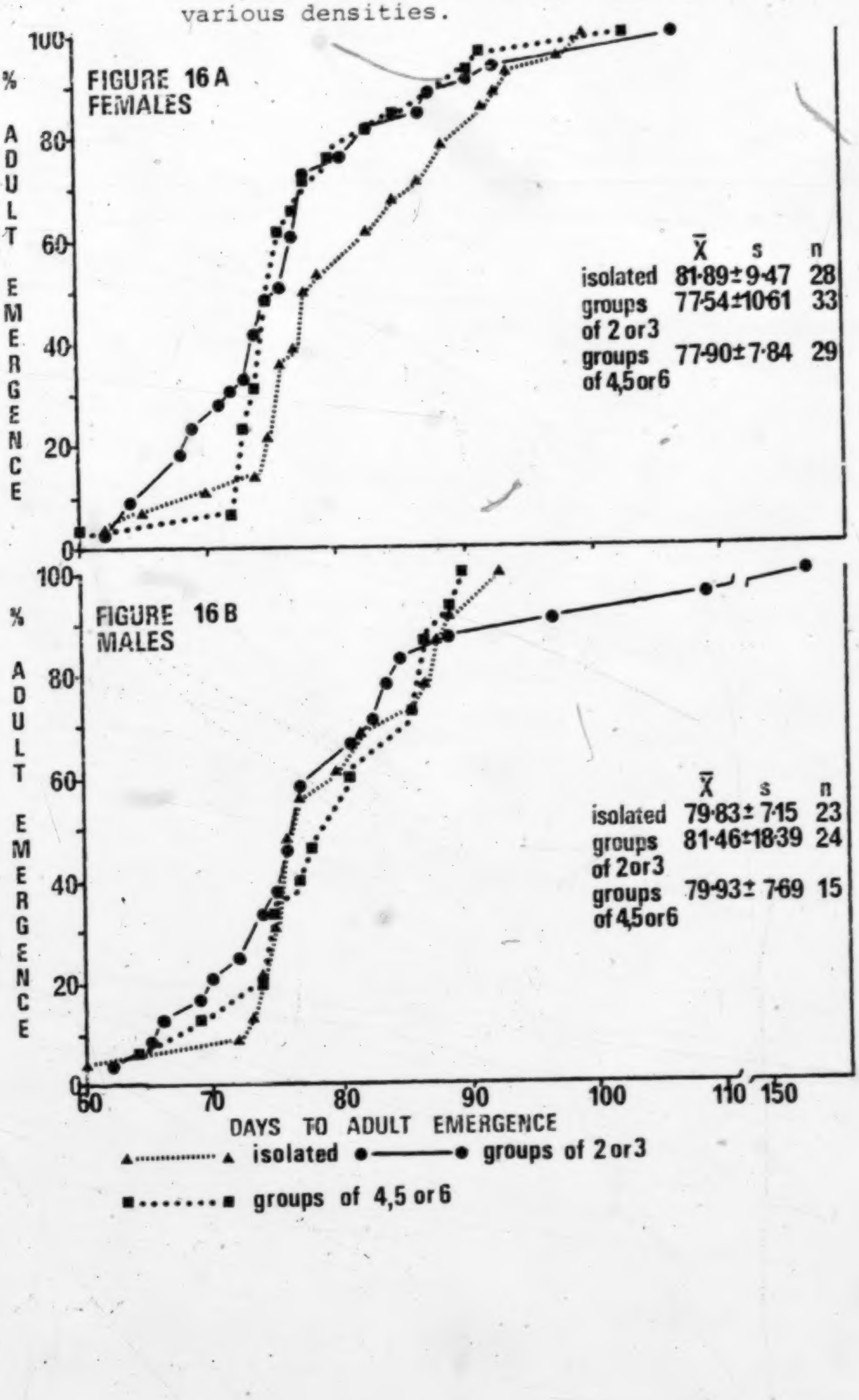


Table 25

Experiment 16, mean weights in mg (± standard deviation) at 48 days of nymphs of *G. veletis* from southern Alberta.

	Isolated	Groups of 2 and 3	Groups of 4, 5 and 6
Females			
	349.20±93.82	369.29±120.04	370.36±92.50
sample size	29	23	32
Males			
	295.73±77.40*	320.45±121.04	295.21±110.93
sample size	31	29	26

*Significantly lighter than isolated female nymphs ($P<0.05$).

was little mortality among singly-reared nymphs (Table 26), but more occurred in groups, the proportion increasing with group size. The male to female ratio was 1:1 among isolated nymphs, 0.84:1.00 in groups of 3 and 0.38: 1.00 in larger groups (Table 27).

There were some nymphs in each treatment which were too immature to be sexed when weighed. It was this class which suffered most mortality after weighing. Since 13 out of 17 such nymphs in the isolated treatment matured as males and only 2 as females, it seems likely that most if not all of the small nymphs which died in other treatments were males also, with death being due to predation by larger nymphs, or to harassment. No nymphs too immature to be sexed at 48 days survived to maturity in larger groups.

The assumption that all deaths were of males gives a perfect 1:1 sex ratio in the experiment as a whole. I made this assumption in calculating the potential number of each sex in each treatment and emergence data was graphed as a percentage of these probable totals (fig. 17). Since all treatments showed some mortality, none of the lines reaches 100%. On this basis, females in larger groups emerged significantly faster ($P<0.01$) than those in other treatments. Only 12 out of a probable 23 males in that treatment matured, so that although the survivors had a shorter mean developmental period than did males in other treatments, the value cannot be accepted as representing the whole population.

Table 26

Experiment 16, mortality of nymphs of G. veletis from southern Alberta in late instars between 48 days and adult emergence.

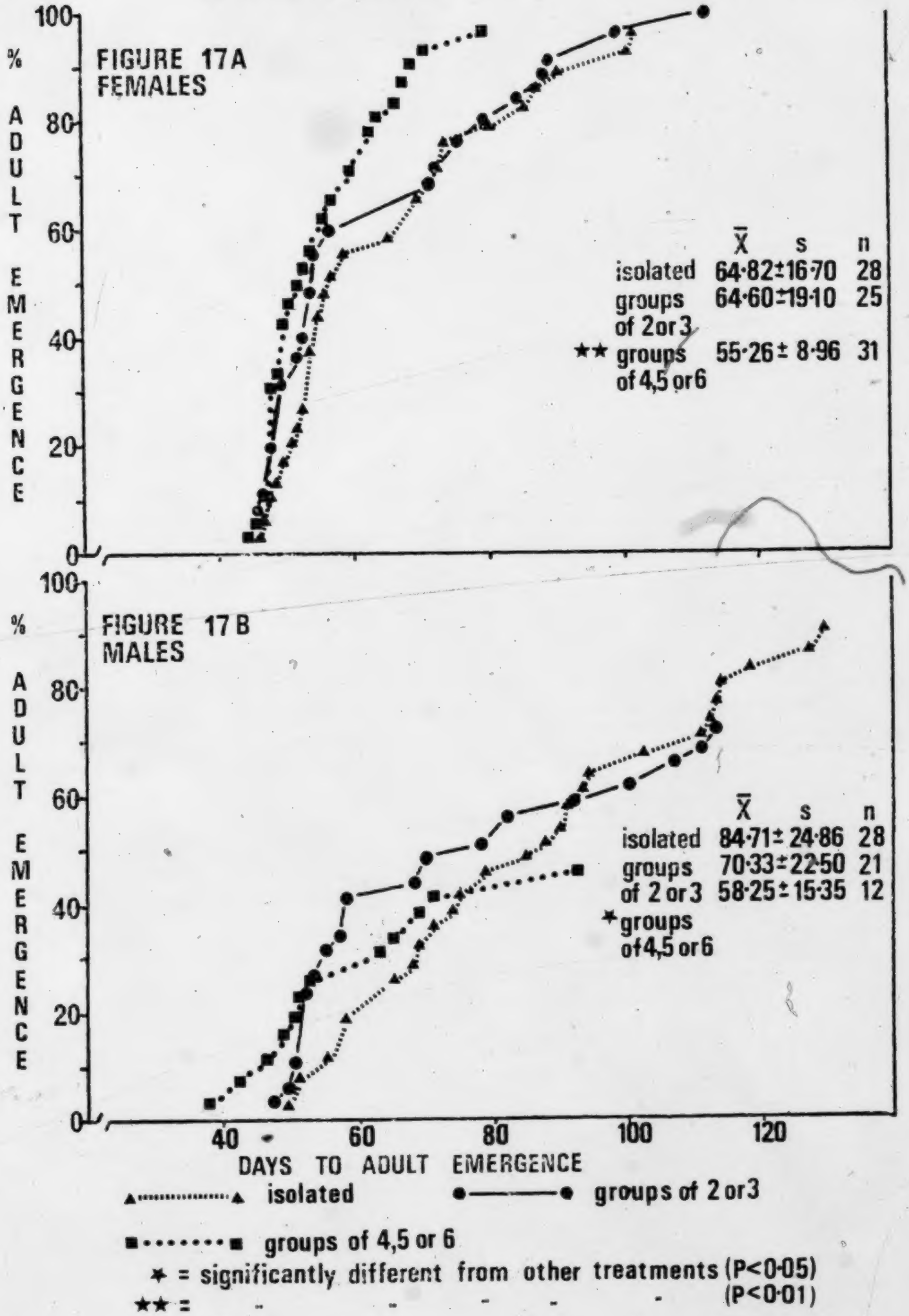
	Isolated	Groups of 2 and 3	Groups of 4, 5 and 6
Males	1	1	1
Females	1	0	1
Unsexed	2	7	13
Total	4	8	15

Table 27

Experiment 16, males and females of G. veletis from southern Alberta emerging as adults.

	Isolated	Groups of 2 and 3	Groups of 4, 5 and 6
Males	28	21	12
Females	28	25	31
Total	56	46	43

Fig. 17. Cumulative adult emergence (days) in Experiment 16, on development of individuals of *Gryllus veletis* from southern Alberta, in isolation and in groups of various densities.

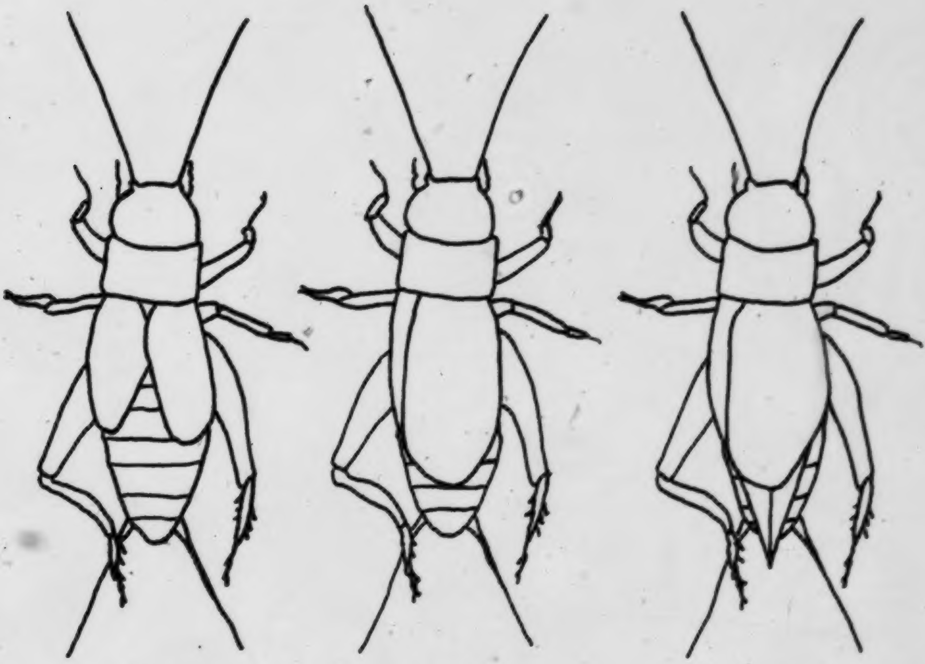


When results are compared for the two stocks of *G. veletis* it can be seen that emergence began earlier in the stock from Alberta (figs. 16 and 17). Mean female developmental period is about 20 days shorter but that of males is not. In fact, when emergence curves for Experiments 15 and 16 are compared, it can be seen that male emergence patterns differ considerably, even for isolated nymphs. Males in 16 (fig. 17B) emerged over a longer period than those in 15 (fig. 16B), so that the slope of their lines is less steep.

Bigelow (1960) reported that nymphs from *G. veletis* populations from Quebec matured faster than those from Maryland and Virginia, and that hybrids between northern and southern populations matured at an intermediate rate. He concluded that growth rate is genetically adjusted to ensure that nymphs are in the overwintering late instars at the appropriate time of year. My data supported this hypothesis, although the last individuals in both experiments took about the same period to mature.

3.8.3.2. *Wing Polymorphism*: As adult *G. veletis* from Indiana emerged in Experiment 15, I noticed that the population showed wing polymorphism. The three wing conditions I found are illustrated in figure 18, adapted from Alexander (1968). His caption applies equally well to my data. As Table 28 shows, most adults reared in isolation were brachypterous, and lacked functional hind wings. In contrast, group-

Fig. 18. Wing states in adults of *Gryllus veletis*.



neotenic brachypterous macropterous

Left, a very short-winged adult male, unable to stridulate, found in a laboratory population: center, the usual macropterous male with normal tegmina: right, a macropterous male (note tips of long underwings), produced in the laboratory. Only the last two are known in field populations. (Alexander, 1968).

Table 28

Experiment 15, wing polymorphism in isolated and grouped individuals of G. veletis from Indiana.

	Isolated***		Groups of 2 and 3		Groups of 4,5 and 6	
	Males	Females	Males	Females	Males	Females
Macropterous	3	5	20	27	8	22
Brachypterous	18	21	1	3	4	3
Neotenic	2	0	2	3	0	3

*** =significantly different from subjects in other treatments (P<0.001).

ed individuals mostly became macropterous. The difference between treatments was very highly significant. Neotenic individuals occurred in low numbers in all three treatments.

The same wing polymorphism occurred in G. veletis from southern Alberta (Table 29), and there was also a highly significant correlation with treatment. Brachypterous adults occurred in substantial numbers only in the isolated treatment, which also produced many more neotenic individuals. However, a high percentage of macropterous adults also occurred in the isolated treatment, in this experiment, which was not found in the study on the population from Indiana.

As Table 30 shows, adults of G. pennsylvanicus were rarely macropterous in any treatment. However, the small number which did appear were females in small groups. There was wing polymorphism among adults of G. fultoni also, but the significance of the phenomenon was not recognized and I did not record whether it was correlated with grouping in this species.

Macroptery associated with grouping was found by Fuzeau-Braesch (1961) in adults of G. peruviensis and G. argentinus. Only females of G. peruviensis showed the correlation, in which grouping increased macroptery from 41% to 84% (with sample sizes of 12 and 19 respectively). Macroptery in samples of G. argentinus increased from 8% to 39% with grouping (sample sizes 25 and 41 respectively).

Table 29

Experiment 16, wing polymorphism in isolated and grouped individuals of *G. veletis* from southern Alberta.

	Isolated ***		Groups of 2 and 3		Groups of 4, 5 and 6	
	Males	Females	Males	Females	Males	Females
Macropterous	13	18	14	23	9	29
Brachypterous	7	8	4	0	1	1
Neotenic	8	2	2	1	1	0

*** = significantly different from subjects in other treatments ($P<0.001$).

Table 30

Experiment 14, wing polymorphism in isolated and grouped individuals of *G. pennsylvanicus*.

	Isolated		Groups of 2 and 3		Groups of 4, 5 and 6	
	Males	Females	Males	Females	Males	Females
Macropterous	0	1	0	4	0	0
Brachypterous	36	15	24	16	13	20
Neotenic	0	0	0	0	0	0

Adults of *Scapsipedus marginatus* (Gryllidae) were never macropterous except when reared in groups, when 63% of 99 individuals in one experiment, and 77% of 62 individuals in another, developed hing wings. The percentage as higher in females than in males.

Saeki (1966a) found that up to 80% of grouped females of *S. aspersus* were macropterous. The percentage was lower among males. Since isolation by wire gauze, or antennectomy, almost eliminated such development, he concluded that the influence on wing development was mediated by tactile stimuli.

These are the only species in which macroptery has been related to grouping in the offspring of unselected stocks. However, McFarlane (1966a) found that if he selected for macroptery by cross-mating only winged adults of *Gryllodes sigillatus* for three generations, the selected stock produced 45% (10 out of 21) fully winged adults, when reared in groups, and only 7% (2 out of 28) when reared in isolation. But this correlation was not found in unselected stocks, and indeed, in one of his experiments, 41% of singly reared adults were macropterous, while in another only 35% of those reared in groups were.

Sellier (1954), working with *G. campestris*, showed that macropterous wing development could be stimulated by implanting brains from young nymphs into older ones, and Mathad and McFarlane (1970) showed that macroptery in

Gryllodes sigillatus was correlated with release of neurosecretory granules from the median neurosecretory cells, while the same cells in brachypterous last instar nymphs were full of granules. Thus wing development in crickets seem to be directly related to brain hormone produced during the latter part of nymphal life.

The occurrence of neotenic adults may be a more extreme example of the same phenomenon. It seems likely that such individuals are the result of premature decline of hormone level, one instar before it usually occurs. These individuals thus become adult before they reach adult size.

Neotenic males are apparently infertile, and I have never succeeded in obtaining offspring from normal females paired with such males. Neotenic females, which have a short ovipositor, do not lay eggs. Both sexes behave like normal adults, and many neotenic males make stridulatory movements and court females, although their wings do not overlap, and they can produce no actual sound. Adult females ignore them, and adult males to not respond to their attempts to challenge them, so that neotenic males cannot establish and maintain territories.

I originally thought neoteny was the result of inbreeding when it first appeared in Experiment 15, but since it also appeared in offspring of field caught mothers, it may be a response to laboratory conditions, and be environmentally induced. Such individuals, as Alexander (1968) noted, have never been captured from natural populations. Saeki (1966b) found that macroptery occurred (only in grouped individuals) under long (16 hour) day length conditions much more than under short day lengths (about 78% as contrasted with 20-25%). Alexander (1968) found that gradually increasing day-length from 12 to 17 hours during development caused all adults of G. interger to be macropterous, while decreasing day-length from 12 hours to 9 suppressed appearance of macroptery completely. Tanaka, Matsuka and Sakai (1976) found that any change in photoperiod in the middle of development, in either direction, increased macroptery in grouped samples of Pteronemobius taprobanensis (Walker) (Gryllidae). They did not rear isolated individuals.

It thus seems possible that the differing frequencies of macroptery evidenced in Experiments 15 and 16 may be related to differences in photoperiod in these experiments. No light cycle was used in either experiment, but lights in the incubator were switched on when I inspected the progress of the experiments. Sometimes they remained on until the next day's inspection, so that nymphs were subjected to intermittent long days and very short ones.

In order to determine if other factors interact with grouping to increase macroptery in G. veletis adults, it would be necessary to carry out rearing experiments with a range of photoperiods.

An experiment carried out under controlled humidity and light cycles using nymphs of both northern and southern populations in one experiment would be necessary to determine whether these are genuine differences between nymphs from the two areas. If members of northern populations really do have a greater tendency to macroptery, it may be related to their inhabiting a harsher environment than do southern populations. Adults emerge in May in the northern part of the range, and probably have a smaller variety of food plants available to them than would be found in Indiana in June or July. Thus mobility could be a greater asset to northern populations than to southern ones, regardless of population density.

Why crowded females of northern populations should mature earlier than isolated ones while crowded males do not is difficult to explain. Male emergence period completely overlapped that of females in the experiment, so that females would be likely to find a mate whenever they emerged. This may be an advantage to the population. Earlier female maturation would be selected for in northern populations, since earlier egg-laying would result in more nymphs reaching the overwintering instars before winter in years when snow came early. Southern Alberta is at the northern edge of the range for the species. In southern populations, early egg-laying might result in adults maturing before winter, which is apparently fatal in this species.

3.8.4 Summary

1) There was no difference in growth rate between isolated and grouped nymphs of *G. fultoni*, *G. pennsylvanicus*, or *G. veletis* from Indiana.

2) Females of *G. veletis* from Alberta stock grew significantly faster in groups of more than three than they did in smaller groups or in isolation ($P<0.05$). Their mean developmental period was shorter than that of females of Indiana stock regardless of treatment. Males showed no difference in growth rate associated with treatments, but they emerged as adults over a longer period than did nymphs from Indiana stock, and their mean developmental period was no shorter.

3) Mortality in males of *G. pennsylvanicus* and *G. veletis* increased with increase in population density and was considerable in groups of six.

4) Macroptery was strongly induced by grouping in both sexes of *G. veletis*. The correlation was stronger in stock from Indiana than from Alberta, which were more likely to be macropterous under any rearing conditions. However, this difference may be related to differences in experimental conditions, rather than to genetic differences between stocks.

5) Neoteny was related to rearing in isolation in *G. veletis* stock from Alberta.

3.9 General Discussion and Conclusions of Section 3 and of the Study

The results reported in Section 1.0 indicated that nymphs of *A. domesticus* are likely to be found in groups in their natural environment. The results of experiments in Section 2.0 showed that actual presence of other nymphs was necessary to increase growth rate to its optimum. It may be assumed that, in most populations, nymphs will be in a group throughout their lives. They will forage independently, but return to the same resting sites regularly throughout development.

Results of Experiments 9 and 10 indicated the circumstances under which living in a group will promote optimum development. It was evident that nymphs grow fastest if they are in contact with nymphs of their own age and size. Such contact, over the first half of development, is enough to optimize growth rate for the rest of the nymph's life. Contact with a larger nymph does not promote optimal growth even in early instars, and becomes inhibitory in later ones, but contact with a younger nymph has no effect on growth rate of the older nymph, so that inhibition was not reciprocal. McFarlane's recent results (1978) indicated that contact with waste products of older nymphs also inhibited growth rate.

The life-cycle of *A. domesticus* in wild populations is known from the work of Bate (1969, a, b, 1971, 1972), who studied two populations in refuse dumps in England. Her results indicated that crickets were usually found grouped and that their distribution within the dump was restricted by dump-structure and temperature. The crickets usually lived in crevices and tunnels within the refuse, at temperatures of 5 to 37°C (mean temperature, 25°C). There were two peaks of adult emergence in summer at different times in the two populations, when emigration from the population by flying occurred, especially of females. However, larger instars could be found at all times of the year.

The only other relevant ecological study in the literature is of the black headed cricket, in Pakistan (Ahmed and Ghauri, 1953). This cricket is A. hispanicus (Ghouri, 1961), a species closely related to A. domesticus. The population had three to four generations per year and the crickets aggregated in cracks in the soil, from which they emerged at night to feed, often severely damaging crops. In this situation there appeared to be less overlap between generations. However, as in the British population, maturation rate varied with temperature and there was no specific overwintering or aestivating stages.

One may now consider how results of my experiments relate to the life of crickets in a natural population. The growth rate of a nymph is optimized if it is able to avoid contact with adults. In a natural population, it seems probable that this would be achieved by younger nymphs actively segregating themselves in crevices too small for adults to enter. Thus, in an uncrowded population, all nymphs could associate mostly with peers and so avoid predation and inhibition of growth. Bate (1969a) rarely found members of early instars (first to fourth) in her attempts to sample populations, which suggests that these young nymphs did not associate with older ones. However, larger nymphs and adults apparently occupied the same parts of the dump. She did not mention any separation of the population by size classes. Such segregation might be difficult to observe during disturbance of the population.

Ahmad and Ghauri (1953) described the annual cycle of population build-up and crash which they observed during their study. Conditions for oviposition and hatching were favourable in late March and early April, in irrigated wheat fields, and the population rose steeply, scattered throughout the fields in innumerable cracks in the moist soil. Then irrigation ceased and nymphs were forced to crowd together in much smaller areas along water courses. In July, Jowar cultivation provided suitable breeding sites of the crickets which were becoming adult then, but the areas were much smaller than the wheat fields and together with the high temperatures, this brought about a population crash. Later, the much smaller autumn population moved to wheat and sarson fields.

If such a cycle occurred in a population of _A. domesticus_, and inhibition of nymphal growth by older nymphs and adults occurred as it did in Experiments 10 and 11, optimum growth rate would be found only in earliest-hatching nymphs, which would be grouped with peers in favourable conditions in the fields. Later-hatching nymphs which would be smaller, would be disadvantaged as the population concentrated near water courses. Their growth rate would be slower, and they would be more likely to be killed before maturation, because they would have less chance of avoiding the larger, older members of the population. The presence of the younger nymphs would not reduce the growth rate of the older ones, which would benefit from inhibiting the development of the rest of the population. The earliest maturing adults would have a competitive advantage over slower-growing individuals in competition for oviposition sites. This would be further enhanced by a short pre-ovipositional period. As a result, their offspring would be further advantaged over those of the slow-maturers, and would be more likely to survive in the next generation. Given favourable conditions, faster maturation would allow an extra generation a year.

of suitable habitat the initial contacts might come about only by chance. I have no information on the distance over which the aggregating pheromone or pheromones operate. If a small population were occupying an area previously occupied by a large one, the fact that it might all be equally contaminated by stable deposits, from the previous occupants, might hinder aggregation of nymphs. However, in this situation the attraction of nymphs for each other might have value in maintaining groups. The fact that stimulation from other nymphs does not have to continue throughout nymphal life to optimize growth rate

The fact that nymphs whose growth rate had been slowed in later instars by the presence of an adult were heavier at maturation than those which grew either in peer groups or in isolation may indicate a possible compensatory benefit to offset the disadvantage of slower growth. Heavier crickets might be potentially better able to survive adverse conditions than lighter ones, and to produce a larger total number of eggs.

The attraction of nymphs to each other and to the aggregation pheromone would tend to draw nymphs into contact with each other even at low population densities, so that nymphs would be unlikely to grow up in isolation even if there were very few crickets in the environment. However, if a small population were occupying a large area would mean that nymphs might still be able to benefit from each others presence. This would be especially true of females, which respond to each other's presence later in development as well as in early instars. Female growth rate is more consistently influenced by the presence of other crickets anyway, and they receive more benefit from such contact, as results of Experiments 8 and 11, and Section 3.6 showed. This reflects the importance of females as migrants, and producers of the next generation. Bate (1969a) found that there was a preponderance of females in the adult population in the refuse dumps she examined, suggesting that the somewhat slower males were more likely to be killed during development than were females.

The fact that females most strongly retarded in growth by isolation (Experiment 11, Section 3.7.4) retained functional wing-muscles for an unusually long period is probably adaptive to periods of very low population density. Females under such circumstances might have to fly a relatively long distance to find a mate or a suitable site for oviposition.

_A_. _domesticus_ is a tropical species which has invaded temperate zones. It has done this by making use of localized pockets of relatively high year-round temperatures, associated with a supply of food. These habitats are almost all created by man.

The characteristics of gregariousness and the way in which food consumption and growth are influenced by it has been advantageous to the species in this adaptation. The warm environments are usually small and patchily distributed, so that exploitation of them is improved if nymphs actually benefit from aggregation rather than being adversely affected.

These responses to aggregation probably developed in members of this species in its original warm habitat, which was probably as a tropical crop pest. Many crop pests are gregarious, examples including grasshopper and locust species, aphids and lepidopterous larvae (Brossut. 1975).

Artificially aggregating a non-gregarious species such as G. veletis indicates how faster growth rate in groups would be selected for, since mortality increased sharply in grouped nymphs, and the nymphs killed were growing more slowly than the others. In the experiments carried out, this was apparently especially detrimental to males, since they tended to be smaller than females.

However, aggregating G. pennsylvanicus, which is found in groups under natural conditions, also increased nymphal mortality, and did not result in faster growth of grouped nymphs. It may be that in this species, which overwinters as eggs, early maturation has detrimental effects on reproductive success. Perhaps eggs which go into diapause long before cold weather begins are more likely to die or be eaten by predators than those laid later.

Perhaps faster growth rate in groups does not have much selective advantage for an individual unless it is associated with a life-cycle which is not linked to the temperate cycle of seasons. One notable difference between the *Gryllus* species examined and *A. domesticus* is that the former are univoltine, but *A. domesticus* has a variable number of generations a year depending on environmental conditions.

It is interesting too that *G. pennsylvanicus* did not show any significant tendency to macroptery. Macroptery was a specific reaction to grouping in *G. veletis*, indicating a clear relationship between crowding and dispersal. All adults of *A. domesticus* are winged, even if reared in isolation, and it may be presumed that the genetic mechanism producing macroptery has become fixed in this species due to frequent need for migration from crowded populations. But adults of *G. pennsylvanicus* rarely developed hind wings in experimental situations, and they are usually brachypterous in the field. Migrations of this species have been described to me in which many nymphs have been seen moving on foot, in swarms, across roads and fields, like locust hoppers. It may be that this is the principal dispersal mechanism of this species.

4.0 SUGGESTIONS FOR FURTHER WORK

4.1 Behavior

Further investigations could be made on the gregariousness of nymphs. Nymphs in groups are vulnerable to intraspecific predation when they are moulting. Does gregariousness disappear at these times? Do younger crickets actively avoid contact with adults? In an experimental arena such as the one I used, would nymphs of various ages form one group, or segregate according to size?

4.2 Stimuli Affecting Development

An experiment in which nymphs could receive olfactory cues from other crickets but not be in contact with them would indicate whether there is any significant pheromonal component in the stimulus to faster food consumption and consequent faster growth.

4.3 Adaptive Significance of Response to Grouping

No work has been done on the effect of grouping or isolation during development on total fecundity or longevity of females nor on their response to courtship. It would also be interesting to do more work on the development and regression of wing muscles in relation to rearing conditions, and on the relationship of long-persisting wing-muscles to glandular function, hormone levels and vitellogenesis.

More work could be carried out on the responses of Gryllus species to grouping, especially on how G. pennsylvanicus responds if reared at a lower temperature. The relationship of macroptery to population density and other factors could be examined in detail in several Gryllus species.

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BIOGRAPHY

I was born on September 22nd, 1943, in Harpenden, Hertfordshire, England, the daughter of a dairy farmer. I grew up in the same place, and attended St. Alban's Girls Grammar School. I did my undergraduate studies, with biology and geography as my principal subjects, at Keele University, in Staffordshire, England, and received a B.A. (Keele) in 1966.

My first job after graduation was as assistant experimental officer to Dr. C.G. Butler, in the Bee Department at Rothamsted Experimental Station, in Harpenden, Hertfordshire, and my interest in insects began at that time. I took a master's degree programme at Birkbeck College, London University, most of which was taught by Dr. R.F. Chapman, and obtained an M. Sc. in 1970.

I worked for two years as an abstracter and assistant editor of "Entomology Abstracts", and began work on a Ph.D. at the University of Alberta, in 1972.